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## THE PROPERTIES OF THE VISUAL EXCITATION-CURVES

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A graph which is built upon the explicit assumption that a certain quantity is to be held constant can convey no information about any changes which presuppose that this quantity is also variable. Many studies which have been made of vision often seek to extract information from a graph respecting some property which had already been definitely assumed to be constant. A function such as

$$V = 32t$$

describes how a body falls. This function is linear and one can see readily that the area under this curve, between given limits, embodies or represents the total distance traveled by the falling body. The ordinate of this curve represents the instantaneous velocity of the object, while the slope of the curve embodies the acceleration of the object.

In the study of the phenomena of vision the fundamentally illuminating experiments are those of intensity discrimination and of acuity. In many of the early attempts to measure the ability of the eye to detect intensity changes and acuity changes one finds the effort made to extract information about intensity discrimination from graphs which were derived through keeping intensity constant. The converse is also often made, when persons seek information regarding frequency discrimination from experimental data gathered when frequency was held constant.

The excitation and the Elementarempfindungen curves are graphs which were worked out by taking certain arbitrarily chosen primaries. The ordinates represent the amounts or the numbers of the units of the chosen primaries; the area under the excitation curve will (and does) represent luminosity or,

if one prefers, the number of functioning rods and cones while the slope of the curve depicts hue discrimination or the magnitude of the change in hue that a given eye can detect. In the case of the excitation curve we can readily interpret both the instantaneous value of the function, and the area underneath the curve and also the slope of the curve in terms of visual discriminations, just as readily as the physicist can assign physical meanings to the corresponding properties of the curve depicting the behavior of a falling body.

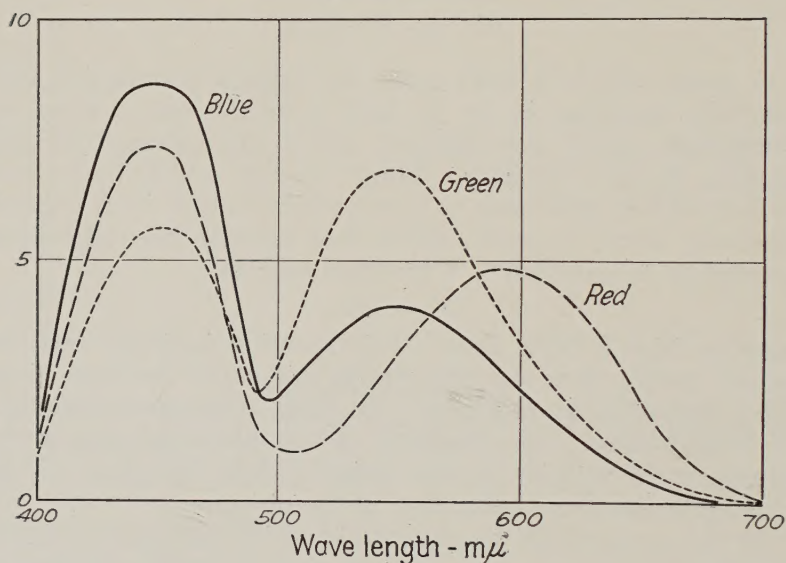


Fig. 1. Helmholtz's three fundamental primaries.

In the study of vision the following facts are explainable if the axis of abscissae be variable wave length: (1) color-blindness; (2) luminosity or brightness; (3) color-mixture phenomena; (4) hue-sensitivity; (5) hue-discrimination; (6) white complementary color pairs; (8) saturation; and (9) minimal hue detection. The facts are explainable without bringing in anything regarding a variation of intensity as will be seen later and much more fully in subsequent studies. The visual psychological properties that are interpretable in terms of varying intensity of the light stimulus constitute another distinct group. In explaining the above group we keep the intensity constant and vary only the wave length.

As the excitation curves are given us by Helmholtz (1) (see Fig. 1) and many others, it is impossible to read off from them the nine psychological characteristics mentioned above. Hecht (2) recognizes that it is possible to apply a simple homogeneous linear transformation to these historic excitation curves and so transform them that they will give the above-mentioned items of information regarding the nature of the visual process. Since these excitation curves are not the direct product of experimental data, a certain non-uniqueness belongs to them as the result of a mathematical operation upon other functions which *were experimentally determined*. Those who set up the excitation curve for us were not restricted in their

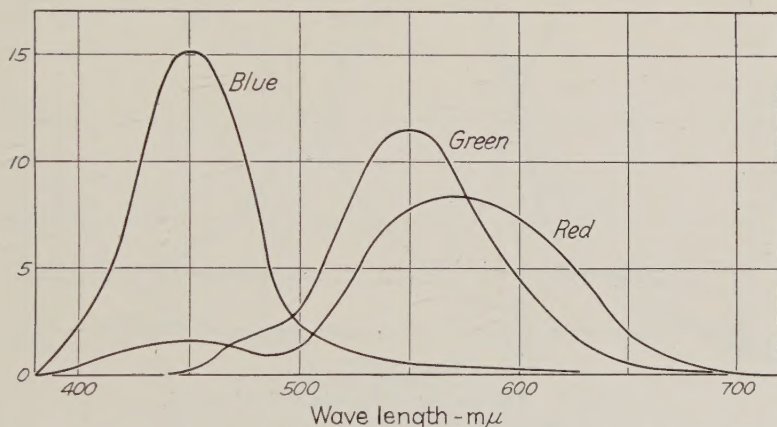


Fig. 2. The curves as determined from the data of Wright.

choice to any particular set of three primaries. If, for example, one takes the curves of Wright (3) (see Fig. 2), he can apply his mathematical technique of transformation to an infinite number of, sets of three, assumed or pseudo-primaries. There is only one restriction which operates to prevent the absolute freedom of choice of the three new pseudo-primaries. This can be illustrated thus: Suppose that *Wright* took B, G, and R to be his primaries and that the *reader* chose to take colors x, y, and z to be his primaries where x, y, and z are thus defined:

$$\begin{aligned}x &= a_1 B + a_2 G + a_3 R \\y &= b_1 B + b_2 G + b_3 R \\z &= c_1 B + c_2 G + c_3 R\end{aligned}$$

In this transformation the new primaries are *functions*, (not arithmetical numbers), of the red, green and blue that

were primaries, for example, as postulated by Wright. One can again state the new or pseudo-primaries as connected up with still other primaries as:

$$\begin{aligned} u &= l_1 x + l_2 y + l_3 z \\ v &= m_1 x + m_2 y + m_3 z \\ w &= n_1 x + n_2 y + n_3 z \end{aligned}$$

Such transformations show that any set of three colors can be taken as primary provided that in making the transformation the determinant in the denominator does not vanish.

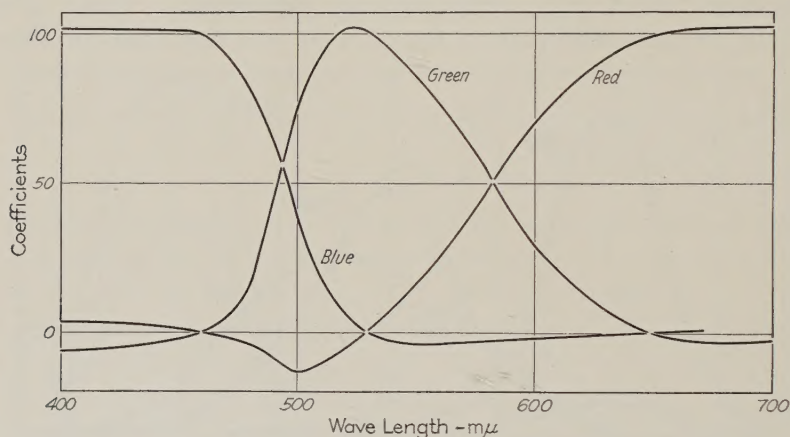


Fig. 3. The curves of Koenig and Dieterici.

Suppose that we solve for B in the set of equations just given,

$$B = \frac{\begin{vmatrix} x & a_2 & a_3 \\ y & b_2 & b_3 \\ z & c_2 & c_3 \end{vmatrix}}{\begin{vmatrix} a_1 & a_2 & a_3 \\ b_1 & b_2 & b_3 \\ c_1 & c_2 & c_3 \end{vmatrix}}$$

If the determinant in the denominator vanishes, then we find that we selected as a primary, a color which cannot serve as such in this set of equations got from the original experimental curves. In the function, which defines x, y, and z the symbol

B = a certain unit amount of blue,  
 G = a certain unit amount of green,  
 R = a certain unit amount of red.

The primary  $x$ , where, to be specific,  $x$  is say  $\lambda = 500$  m  $\mu$  of the given spectrum, might be thus represented,

$$x_{500} = 50R + 250G + 75B,$$

that is, it takes 50 units of  $R$  plus 250 units of  $G$  and 75 units of blue to match the color of  $\lambda = 500$  of the spectrum which is being matched. Similar equations would tell how to duplicate the remaining two primaries, namely,  $y$  and  $z$ .

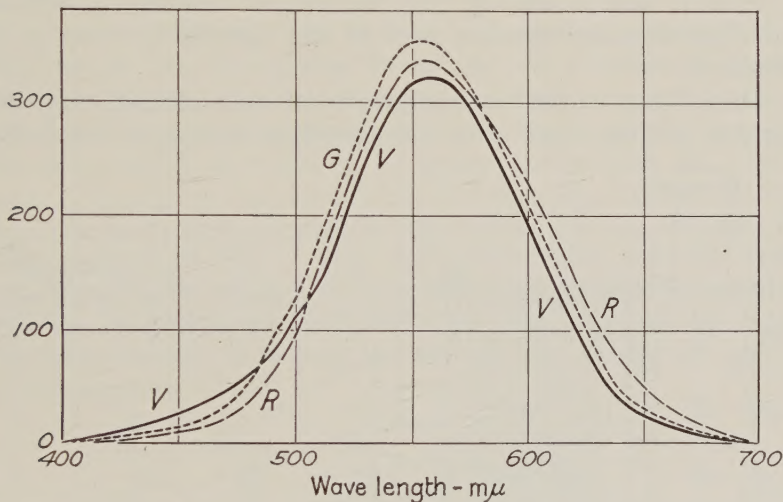


Fig. 4. Hecht's transformed excitation curve.

Again suppose that one knew both that  $450 \text{ m } \mu = 102B + 2G + 4R$ , and that

$$B = [(a_1)x + (a_2)y + (a_3)z]$$

$$G = [(b_1)x + (b_2)y + (b_3)z]$$

$$R = [(c_1)x + (c_2)y + (c_3)z]$$

it then follows that

$$450 \text{ m } \mu = 102 [(a_1 + b_1 + c_1)x] + 2 [(a_2 + b_2 + c_2)y] - 4 [(a_3 + b_3 + c_3)z].$$

Thus one demonstrates that it is possible to get an infinite number of sets of equations of  $x$ ,  $y$ , and  $z$ . The student must, therefore, be alert to note whether or not the equation describes the primary of the experimental curves or of the transformed curves. By making such a linear homogeneous transformation the student of vision can move backwards or forwards from any set of three (primaries) to any other.

## EXCITATION CURVES

These excitation or sensation curves were first obtained experimentally through mixing colors. Some spectrum was taken as standard and then through a process of matching, using only three different colors, this entire spectrum was duplicated. This process can readily be sensed by the reader from Fig. 5. Here is a three-fold source of light and it is easy to project, upon a screen, such amounts of the three colors as will duplicate any desired part of the spectrum assumed as standard.

Since these curves are the graphs of data embodying color mixtures which occur when the spectrum which we used was

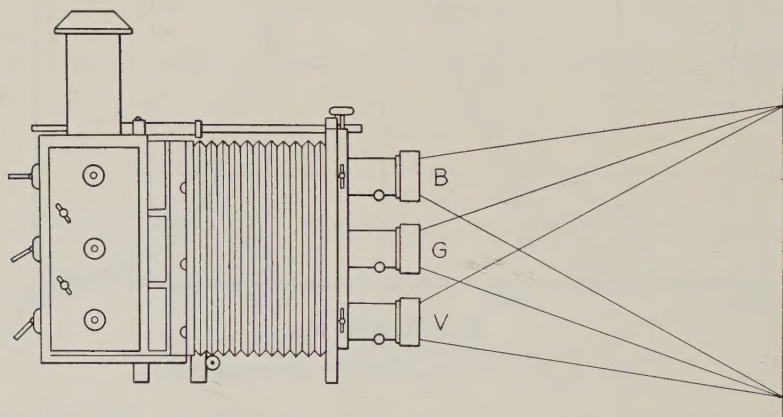


Fig. 5. A method of mixing colors so as to duplicate a standard spectrum.

a constant energy spectrum or the equivalent, it follows that these three sensation curves do not include variations of intensity. In a preceding section we showed that intensity cannot be represented (save as it is a constant) by means of these curves. Attempts have been made, by some who had not reasoned out very thoroughly the facts in the case, to introduce brightness into these curves. Hecht points out two such attempts (2).

One of these attempts rested upon the assumption that there are three groups of receptors in the retina, but there are not the same number of receptors in each group. Experiments by Judd (4), and others (5) pointed out the fact that some colors are very much more effective in aiding in producing white than others. For example, it takes a great deal more

yellow to cancel violet than it does of wave length 576 m  $\mu$  to cancel 475 m  $\mu$  and again the relative amounts here are very different from what they are for 609 m  $\mu$  and 494 m  $\mu$ . The result of these experiments was taken to mean that the population of the cones is as 1 : 75 : 100. There are said to be 75 green-producing cones and 100 red-producing cones to every one of blue. The other attempt to incorporate brightness into these sensation curves made the assumption that the number of cones of each family is the same as the number of the other two families and that at any particular threshold of stimulation the functioning receptors are distributed among the three families and that in each case where the psychological experience is an experience of white that the cones are functioning in the ratio of 1 blue to 75 green, and to 100 red. Both these attempts to read luminosity or brightness into the excitation curves involves a serious weakness. Let us consider the latter expedient first. This says that there are the same number of cones of each family, but that one sees white when they are excited in the ratio of 1 : 75 : 100. Let us take a few examples here to show how the flaw in this assumption can be made manifest.

| <i>Blue</i> | <i>Green</i> | <i>Red</i> | <i>Experience of the Individual</i> |
|-------------|--------------|------------|-------------------------------------|
| 1           | 75           | 100        | Sees white                          |
| 10          | 750          | 1000       | Sees white                          |
| 14          | 1000         | 1000       | Does not see white                  |
| 600         | 1000         | 1000       | Sees blue                           |

This table can be extended indefinitely. If the individual sees only white when the stimulated cones are in the ratio of 1 : 75 : 100, and if there are equal numbers of cones of each family, it follows, since the red cones are brought into play a hundred times as fast as the blue, that the former will all be called upon to function long before all the blue and green cones are. From that point on until the last cone threshold of the blue shall have been reached, no more red cones can be set into action and as the result of this, from here on there must be a color which is the result of the interaction of the green and the blue. Again, as there are 75 green cones called into action for every one blue cone, it follows again that, as we increase the intensity of the light, all the green cones will have been set into action long before all the blue cones are functioning. When such intensity of light has been reached

which has set not only all the green cones but also all the red cones into action, then with all additional augmentations of the intensity of the light there must be experienced a blue color. This is inevitable because of the predominance of the blue cones activated as over against what is called for by the proportion 1 : 75 : 100.

In this way it is clear that if one would take white light and stimulate the retina, the subject would, at first, see white; then as the light is further increased there will be experienced a hue which is the resultant of the operation of the green and blue cones, as soon as all the red cones will have been set into action. Further increasing of the intensity of the stimulus will be accompanied by an experience of the colors of the violet end of the spectrum as soon as the green cones have been set into action.

This attempt to have the excitation curves incorporate the data of brightness very evidently involves the presence of a fallacy, for the simple reason that as we take white light and stimulate the retina with it we experience white or gray all the way up from light of lowest intensity to light of maximum intensity. Thus this theory that there are equal numbers of cones of each family and that the experience of white is the correlate of the action of these in the ratio 1 : 75 : 100 breaks down. If an individual experiences white all the way up from light of minimal intensity to light of maximal intensity it cannot follow that the population of the cones and their action are as this assumption postulates.

The second assumption still rests on the fact revealed by experiment to the effect that the relative efficacy of the colors in producing white is as 1 : 75 : 100. But how incorporate this property of brilliance into our curves which have been made only to express color-mixture data?

The situation so far is that those who gave us our excitation curves had a multiplicity of units (three). They had a unit of V, another unit of G and still another unit of R. What they then wished to do was to replace these three sets of units by a single unit. The lay of the land at the time can be shown thus. Three possibilities are open to the student of vision. They are: (a) one unit of V, one unit of G, one unit of R; or (b) a common unit of energy; or (c) a unit of brightness. Some writers continued to stumble along seeking to clear up the problems of vision by utilizing the threefold set of units. While

they continued to do this they were unable to introduce into the curves anything more than what they had put into them; namely, color mixture data. Soon numerous attempts were made to introduce or to incorporate other facts into them. Brightness was chosen as one to be incorporated into the curves. The fact that brightness is a property of both "hue vision" and "white light vision" constituted it an outstanding trait of all visual experiences. In the dimmest light and throughout the entire range of moderate intensities as well as at maximal intensities, brightness is an ubiquitous trait. Perhaps it was for some such reason that students early attempted to incorporate this property into their curves. We have already seen that one attempt was made which proved premature. The second attempt made seems to be much more hopeful of meeting with success.

This attempt was made by those who were aware of the experimental findings which showed that violet was much more effective in producing white, when in combination with the other colors, than was either green or red. Carefully made experiments showed that this effectivity for producing whiteness of the various cone groups was as 1 : 75 : 100. One violet cone is as effective in giving white (or gray) as are 75 green cones, or as effective as 100 white cones.

Suppose then that these men assume that the population of the cone groups in the retina is *not* equal in number. This was taken for granted by those who made the preceding assumption. Let us, therefore, accept the ratio 1 : 75 : 100. This seems to be a very reasonable hypothesis. Since one blue or violet cone is as effective as 75 green cones in production of white, then, what is more natural than that there should be 75 times as many green cones as there are violet cones? Likewise, since a violet cone is as effective, in the production of white, as 100 cones of the red producing group, what could be more plausible than to say that in the retina there are one hundred times as many red producing cones as violet producing. On this assumption hue would result from a stimulation of such a magnitude and of such a character as not to stimulate the cones in the proportion of 1V : 75G : 100R. Any stimulation which sets up an imbalance, from the standpoint of this ratio, would produce an experience of hue, and similarly any stimulation, no matter what its intensity (within the limits of the eye's sensitivity), which stimulated the cones in this

ration of 1 : 75 : 100, would give rise to the experience of gray or white. Surely here is an assumption that one is prone to say must be adequate.

Now what about the hypothesis that the total population of the cones of the three groups or families is in the proportion indicated by the experiments on the relative efficacy of the different cones in producing the experience of white? Viewing the matter in an *a priori* deductive fashion one feels confident that the assumption is adequate.

Suppose now we get a red as saturated as we can and then increase its intensity. We can make an intensity discrimination experiment on this red and keep a record of the data. Finally we reach the maximum intensity. No brighter red can be discriminated by the eye than that which results when the light is of such intensity as to set all available cones, of the red family, into action. The brightest red we can discriminate is one which is brought about through the activation of all the cones of this particular family. Another experiment of the same kind can be made with green light and with a similar result and implying the same sort of interpretation. Let us now take a violet or blue and run this through the same type of experiment. If our assumption as to the relative distribution of cones were true, we would be unable to get anything like so many intensity discrimination steps when working with the violet as we do with the other two primaries. If we have only one violet cone to each 100 of the red family cones we could never get so bright a blue as we can a red or green. Likewise in the case of the green. Since brightness is shown to be proportional to the number of functioning retinal elements we could never have a green so bright as the maximum red and by far more would our maximum brightness of the blue fall short.

Experiment contradicts this. We can have a blue as bright as our brightest green or even our brightest red. So falls by the wayside this second attempt at incorporating brightness into the excitation curves. A new attempt remains to be made. It is a very simple matter to contrive a theory of vision that will explain a few detached facts, but what the scientist seeks is a theory that will simply embody or display all that is experimentally gleaned in the laboratory.

Hecht has developed for us a transformed set of excitation curves (2) (see Fig. 4). These were derived originally from color-mixture experiments and the data so gathered were

subjected to a linear homogeneous transformation. This was, of course, the way that both the elementary and the fundamental excitation curves were obtained. The transformation that gave the above figure was the one from which Hecht proposes to deduce the properties of vision that are correlated with a change in wave length and with intensity kept constant.

#### THE NORMAL EYE

If these excitation-curves are to explain all the parts of vision under the restriction that the intensity of the stimulus is held constant, certain requirements with reference to the curves are immediately apparent.

(1) They are to represent three equi-numbered groups or families of receptors. To do this the functions are so transformed that the area under any curve is equal to the area of each of the other two.

(2) The demand is also made by the one setting up these transformed functions that the summed area under all three of these curves taken separately shall add up to give the observed visibility curve of the spectrum. Stated otherwise, this is the same as saying that the *sum* of the area under each of these three curves shall give the observed or experimentally checked visibility curve. It follows, also, incidentally that the total area under the curve which is the sum of the three separate excitation curves will represent the total number of functioning receptors when the *entire* spectrum is applied, and not some monochromatic light.

This second requisite will immediately cast out the experimental curves of Wright (see Fig. 2) as well as the excitation curves of Helmholtz (see Fig. 1) and other transformed functions such as those of Koenig. The visibility curve is a smooth continuous function having but one maximal value. Such a curve can not be got from the excitation curves of either Wright or Helmholtz. If one adds the ordinates of the Helmholtz excitation curves he will find that the resultant curve will have two maximal values and not one as is the case with the visibility curve. Since this is the state of affairs it follows that the elementary and the fundamental curves will not prove adequate to the task of explaining the visual process as a whole.

(3) These curves that we accept must be consistent with the observed hue experience. That is, these curves must tell something about the experience of different colors and also

about the *how much* of the experience. Later on it will be shown that this information will be imparted by adjusting the relative ordinates or heights of the excitation curves.

(4) These curves must also be consistent with hue discrimination. This item of the visual process will be inserted in the *slopes* of the curves. The reader will remember that in the case of the falling body the slope was constant and he will also persistently bear in mind that in this case he has three curves to grapple with, and not just one simple linear function, as in the case of the law of the falling body. *Hue* discrimination is, therefore, to be determined from the slopes of our three excitation curves, whereas observed hue is to be interpreted by the *relative* heights of the curves at any given wave length.

(5) These curves are constructed to describe the normal eye, and they must therefore not be expected to tell all about the vision of the abnormal eye, but there are several things that have been observed about the color blind which suggest the possibility of making significant minor adjustments in the excitation curves describing the normal eye.

(6) Our curves must also embody information regarding white complementary colors. This matter of color complementariness gives another "look in" at color mixture with the result that we find embodied in this phase of the problem of vision that several of the laws of algebra hold and that the numbers involved are of the character of complex numbers involving a real and an imaginary component.

(7) Once one has detected the real nature of what is at work in the experience of white complementariness he is literally forced into the making of a quantitative study of the phenomenon of saturation. Again if the three excitation curves we have settled upon are to be suitable for an adequate theory of vision we must be able to read the facts regarding saturation directly from our curves.

The above seven requirements are made of any set of curves which is to describe our visual experience. Will the three curves of Hecht meet these demands? Evidence of their adequacy is here given in the form of a quantitative analysis of hue discrimination.

## AN APPLICATION OF THE VISUAL EXCITATION CURVES

The function  $V = (32)t$  which describes the behavior of a falling body, displays three distinct bits of information: the instantaneous value of the velocity; the total distance traveled, and the acceleration. In this case the acceleration is zero.

In the problem we are concerned with, we have not one but three curves with which to deal, and it is evident that we have a right to expect them to impart much more detailed information than could possibly be given by a single function. In the case of the function

$$V = 32t$$

we have a constant slope, whereas the excitation functions have varying slopes throughout and further significant properties emerge as a consequence of the fact that they intersect at different points (5). The relative differences of the ordinates of these functions, corresponding to a given wave-length, are quantities which describe the most variable and individual property of vision.

The total area under the three curves (see Fig. 4) is a measure of the total number of functioning retinal elements (2). The area enclosed under the "visibility" curve expresses this number under the condition that prevails when the eye is stimulated by the entire spectrum, while the ordinate is a measure of color mixture, luminosity or of the number of receptors functioning in response to monochromatic light. The *relative* differences between the ordinates corresponding to a particular wave length is found, both through experiments and mathematical description, to be an extremely accurate measure of the experience of hue. The slopes of the curves in turn give us an excellent measure of hue discrimination. These properties are compactly given thus:  $A \equiv \text{area} \equiv \text{number of activated receptors}$ ;  $\frac{dA}{d\lambda} \equiv O \equiv \text{ordinate} \equiv \text{luminosity, etc.}$ ;  $D \equiv \text{relative difference of ordinates for a corresponding wave length}$ ;  $\equiv \text{hue sensitivity}$ ; and  $\frac{d^2A}{d\lambda^2} \equiv \text{slope} \equiv \text{hue discrimination}$ .

Perhaps one of the most telling arguments in support of the three-receptor theory of color vision is brought out clearly by means of these excitation curves. On an average there is a decided constancy of both "A" and  $\frac{dA}{d\lambda}$  as shown by experi-

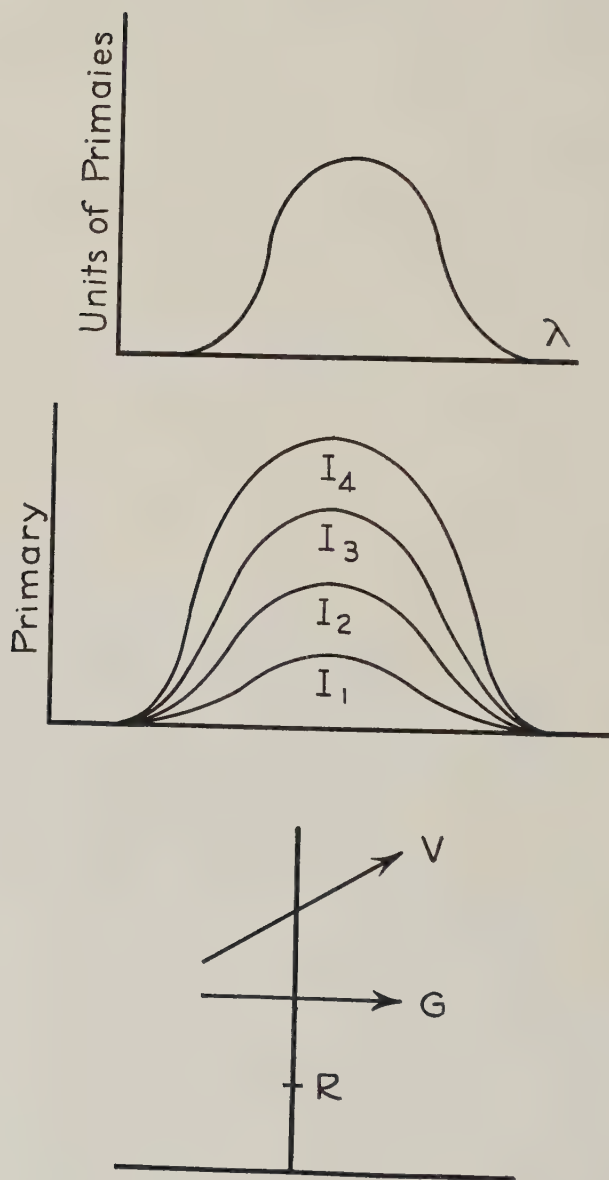


Fig. 6. (Upper). Fig. 7. (Center). Fig. 8. (Lower).

ments on different individuals. Taken in the large the element of individuality of the eye is shown progressively as one passes from the study of  $A$ , to the study of  $\frac{dA}{d\lambda}$ , and then to the study of  $\frac{d^2A}{d\lambda^2}$ . In life we recognize each other as individuals

and accord to each person a uniqueness which makes him an unsubstitutable object. Science washes its hands of the attempt to get the unique, so say many scientists. Yet all know that as the order of the differential equation advances it calls for the positing of more and more initial or boundary conditions. Along just this way lies individuality. The more individual any affair is, the higher is the order of the differential equation. In our present problem we find that the only aspect or property of our curves which can be very greatly changed, relatively, and still leave the areas under the curve virtually unchanged is the slope of each of these curves. We can make a large change in the relative slopes of these curves at almost any point and yet keep our enclosed area a constant. In this respect we have a new light as to how these excitation curves may serve as a realistic account of the retinal physiological processes. The most variable feature about vision is the ability of the eye to make hue discriminations.

Since one of the most variable properties of the eye is its functioning in making hue discriminations it is certainly significant—and a telling blow for the three-element theory—that there is an aspect of the curves that lends itself to great modifications and yet, at the same time, leaves unaltered the total area under the curves. If we had but one curve it would be utterly impossible to do this. However, since we have three curves, each enclosing equal areas, and since these are placed as they are it is perfectly simple to change their relative slopes greatly without affecting the total area enclosed. This variability of the slopes of the three curves then is a trait that can be easily varied, its psychological correlate is given us by the fact that hue discrimination is equally variable from eye to eye. To fit our excitation curves for one eye and then for another, we are called upon only to vary the relative slopes of these curves. We can easily strike a general average that holds for many eyes in terms of  $A$  and  $\frac{dA}{d\lambda}$ . This is but a

way of saying that these two quantities are fairly impersonal. It is not so easy to do this with the quantity  $\frac{d^2A}{d\lambda^2}$ . This quantity tells us something that is quite personal about the eye. It is not evident how we could get this high individual variability characteristic of hue discrimination if we did not have a multiplicity of excitation curves. Again, we say that this is one of the most significant arguments for the adequacy of the Young-Helmholtz theory.

The problem now before us is to check hue discrimination and to say just how it shall be given to us by the curves. (See Fig. 6.) At the two extreme ends the slope of the curve shown in Fig. 6 changes very slowly—hue discrimination is very poor at those places. At the top the slope is quite flat, almost horizontal for some distance; here also the discrimination of hues is very poor. If we were to vary the intensity  $I$  of the stimulus we would find that the curves would be of this general character. (See Fig. 7.) The greater the intensity the flatter the curve would be at the top.

Experimentally what must be done in carrying on a measurement of hue discrimination is to keep the hue intensity,  $L_H(\lambda) = \text{constant}$  and make the change in the hue. If we could not do this our measurements would be meaningless. A table may be helpful, at this point.

| $\lambda_3$ | V  | G  | R  | $L_H$ | $L_w$ | $L_t$ |
|-------------|----|----|----|-------|-------|-------|
| 500         | 40 | 30 | 25 | 20    | 75    | 95    |
| 550         | 45 | 30 | 20 | 35    | 60    | 95    |
| 330         | 43 | 27 | 25 | 20    | 75    | 95    |
|             | 48 | 27 | 20 | 35    | 60    | 95    |

In making readings the student must exercise caution in noting which curve is the lowest in the region where he is taking the measurements. The balanced part of the visual effect is always three times the value of the least ordinate at the wave-length considered. Let us take the cases where

$$\left\{ \begin{array}{l} V_1 = 48 \\ G_1 = 27 \\ R_1 = 20 \end{array} \right\} \quad \text{and} \quad \left\{ \begin{array}{l} V_2 = 45 \\ G_2 = 30 \\ R_2 = 20 \end{array} \right\}$$

$$\Delta H = (V_1 - V_2) + (G_1 + G_2) = (48-45) + (27 + 30)$$

This expression gives us the rates of change of the ordinates for V and for G. The reason that the ordinate of the red curve does not appear is that care was taken to keep the luminosity constant. To be more accurate what is kept constant is the white luminosity. Having found the relative differences of the two biggest components for any given  $\lambda$  and having equated this to H, we may now get the rate of change of hue with respect to wave length by dividing the above equation by  $\Delta\lambda$ .

There results:

$$\begin{aligned}\frac{\Delta H}{\Delta\lambda} &= \frac{V_1 - V_2}{\Delta\lambda} - \frac{G_1 - G_2}{\Delta\lambda} \\ \therefore \frac{dH}{d\lambda} &= \frac{V_1 - V_2}{(d\lambda)} - \left( \frac{G_1 - G_2}{d\lambda} \right)\end{aligned}$$

to the right of the point where we have the first intersection of the lowest curve the variable which will disappear from the equation is V. Thus the measure of hue discrimination for all wave-lengths to the *right* of the point where the Red and Violet intersect will not involve V. The expression for hue discrimination throughout this interval is given by

$$\begin{aligned}\frac{\Delta H}{\Delta\lambda} &= \frac{R_1 - R_2}{\Delta\lambda} - \left( \frac{G_1 - G_2}{\Delta\lambda} \right) \\ \frac{dH}{d\lambda} &= \frac{dR}{d\lambda} - \frac{dG}{d\lambda}\end{aligned}$$

This information can be shown graphically in a way that may help the reader to a better appreciation of how hue discrimination is measured. Let us take a particular ordinate and let points on it indicate the points where it cuts the excitation curves. (See Fig. 8.) At the points V and G are indicated the slopes of the V and G. curves. If these indicating lines are diverging, converging or parallel the hue discrimination will be an increasing, decreasing or a constant function.

From the curves that have been finally accepted as giving a description of the facts of vision it is easy to show from the equations below,

$$\begin{aligned}\frac{dH_1}{d\lambda} &= \frac{d}{d\lambda} (V_\lambda - G_\lambda) \\ \frac{dH_2}{d(\lambda)} &= \frac{d}{d\lambda} (R_\lambda - G_\lambda)\end{aligned}$$

the right hand side of each equation to be a function of  $\lambda$ . From this we have that

$$\frac{dH(\lambda)}{d(\lambda)} = f(\lambda)$$

On this assumption we may say that

$$\frac{\Delta H(\lambda)}{\Delta(\lambda)} \approx f(\lambda)$$

Here we take a certain finite increment of  $H(\lambda)$  and assume it to be constant and at the same time *equal to the least perceptible change* in hue. Since  $\Delta H(\lambda) = \text{constant}$ , it follows that  $\text{constant} \approx f(\lambda) \cdot \Delta(\lambda)$ .

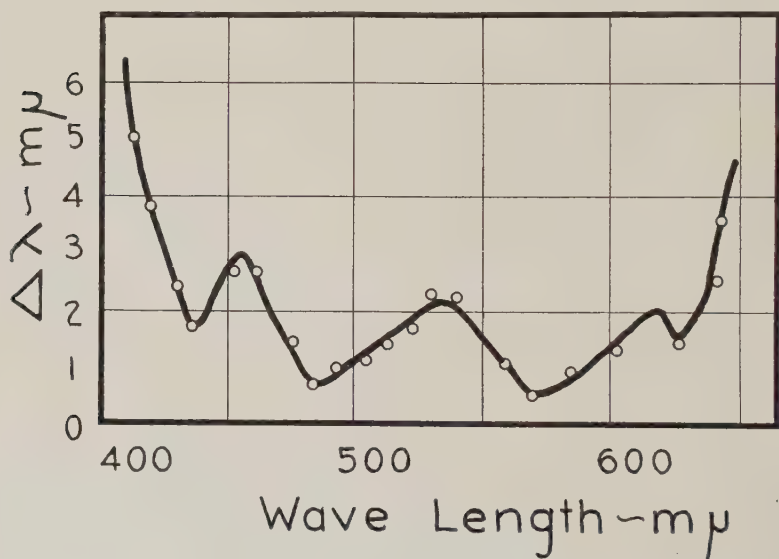


Fig. 9. The data of hue discrimination of Lauren's eye taken from Laurens and Hamilton '29. The smooth curve gives the data, whereas the points are computed from the primaries V, G, and R.

It remains, therefore, only to plot the function between  $\Delta\lambda$  and  $\lambda$  and then to check this curve with the data from experiments. (See Fig. 9.)

The curve here shows a remarkable correspondence between the facts revealed by experiments and the calculated curve is sufficient proof that herein is offered a satisfactory method of measuring hue discrimination.

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 Petroleum in 1934

This volume contains papers and discussions presented before the Petroleum Division of the American Institute of Mining and Metallurgical Engineers at the Los Angeles (September 29, 1933), the Dallas (October 6 and 7, 1933) and the New York (February 19 to 22, 1934) meetings. For necessary clearness these papers are grouped in five chapters. Chapter I considers "Production Engineering and Engineering Research," with 14 papers (100 pages). To mention four important contributions in this chapter: "Properties of Hydrocarbon Mixtures as Related to Production Problems," by W. K. Lewis, in which he shows that by appropriate technique the volume of both gas and oil in the crude flowing from a well can be calculated as a function of the pressure at the point in the producing sand, provided one knows the sand temperature. This being the case it should explain the high gasoline content of high pressure gas caps. A second paper, "A Theoretical Analysis of Water-flooding Networks," by M. Muskat and R. D. Wyckoff, in which the theoretical efficiency of staggered line drive, direct line drive, five-spot, and seven-spot methods of flooding with water to force the oil out into predetermined producing wells is considered. A third, "Recent Changes in Reservoir Pressure Conditions in the East Texas Field," by G. L. Nye and C. E. Reistle, Jr., who endeavor to show that the reservoir pressure is dependent on the rate of production and that with slow production the total recovery would be greater due probably to the slow vertical flooding by natural waters. A fourth, "Basic Data for Oil and Gas Wells," by L. J. Pepperberg and E. A. Stephenson, with an excellent bibliography of 84 titles. Chapter II is "Petroleum Economics," covering 40 pages with six papers, two of which are (1) "Tanker Rates and Canal Tolls as Factors Determining Markets of Foreign Oils," by V. R. Garfias, with comprehensive tables showing costs; and (2) a table, "World Petroleum Consumption," by V. R. Garfias and R. V. Whetsel, covering from 1931 to 1933 inclusive, showing a grand total of 1,366,291 thousand barrels consumed in 1933. Chapter IV (278 pages) covers world production of Petroleum for 1933. The production is given country by country by various authors. The tables include much more detailed information than before; a procedure which is to be followed in the future. Chapter V contains a paper by W. Miller, "Developments in Refinery Engineering during 1933," which is a summary of Refinery development during the year.

This useful volume is a necessary part of all those interested in Petroleum. To those familiar with this series nothing need be said; to those unfamiliar with it, it may be stated that these volumes represent the cream of the Petroleum papers from the Economic and Industrial end.—WILLARD BERRY.

**Petroleum Development and Technology, 1934.** *Trans. Am. Inst. Min. and Metal. Engineers*, Vol. 107, 466 pages; numerous tables and figures. New York, 1934.

## NEWER ASPECTS OF NUTRITIONAL ANEMIA.\*

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Nutritional anemia is a deficiency disease belonging to the physiological types of anemia. Abderhalden (1) in 1899 was the first to demonstrate this type of anemia in white rats fed a sole milk diet. Bunge (2), a year later, showed that milk was notoriously low in iron content. Nothing of value was developed in this regard until Hart (3) in 1925 reported the remission of the anemia by the feeding of iron and copper. He further stated that inorganic iron alone was ineffective, and that green plant material, an alcoholic extract of this material, or chlorophyll itself was essential for the assimilation of the iron. Hill (4) is also of this opinion.

Beard and Myers (5) in 1931 showed that copper was not a necessary adjunct for the assimilation of iron in opposition to Hart's earlier claims. Beard and Myers further stated that other metals (nickel, germanium, arsenic and zinc) would likewise stimulate hemopoiesis. These authors brought forward another point of considerable importance in that they found by doubling the minimum amounts of iron required for the remission of the anemia the time necessary for recovery to occur was reduced from 4 weeks to 1.8 weeks. This is in agreement with the results of Leichsenring and Flor (6) in their studies on infants.

The problem was further complicated when Osata and Tanaka (7), Furniss (8), and Foster (9), each from separate laboratories, found that ultra-violet light stimulated hemopoiesis.

Scott and Erf (10) in 1930 reported the prevention of nutritional anemia in white rats by a special method of feeding the cattle producing the milk. Essentially it was due to the feeding of hay rich in plant pigments and supplemental factors fed to the cows. These same authors (11) later announced that they were able to show a difference in milk obtained from cows which were pasture-fed and those that were fed the ordinary "winter" dairy ration. Hunt and Krauss (12)

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proved that the milk from cows on a green pasture diet had a higher vitamin G content than cows on a dry feed, and that cows on pasture during a vigorous plant growth produced a milk of a higher vitamin G content than those on pasture that was over-mature. Of interest in this connection is the work of Zih (13), who found that rabbits developed an anemia which was not cured by the addition of vitamin B when chlorophyll-free food was used, and the addition of chemically pure chlorophyll, or green food, to the diet caused a rapid return to normal.

Scott and DeLor (14) in 1933 reported rapid hemopoiesis in milk anemic rats by the use of:

1. An iron and copper-free alcoholic extract of alfalfa.
2. Haliver oil.
3. Milk obtained from cows on a special feed in which the hay contained large amounts of plant pigment.

#### DISCUSSION

Early in the experimental work on milk anemia it was demonstrated that factors other than inorganic iron are essential for hemopoiesis. It has been demonstrated that chlorophyll is very similar to hemoglobin in chemical composition. Pryde (15), in his "Recent Advances in Biochemistry," has pointed out that both hemoglobin and chlorophyll possess a common structural unit known as porphyrin. Porphyrin is a complex molecule composed of pyrrol rings. Besides porphyrin hemoglobin contains iron and protein which is called globin. Chlorophyll on the other hand possesses magnesium instead of iron and phytol instead of globin. Just what chemical reaction is involved in the relief of hemoglobin deficiency by a supplemental chlorophyll therapy is not known at present. Perhaps it is not the chlorophyll that is concerned; it may be another factor not yet known, or that chlorophyll may be a catalytic agent. In this respect we cannot neglect to mention carotin, which has been shown by Olcott and McCann (16) to be the precursor to vitamin A. Our experience with crude carotin has been that it has a primary depressant action on the blood-forming organs in rats on a *normal* diet, followed by a gradual return of the blood picture to normal. It may be that certain impurities present in the crude preparation prevented the carotin from exhibiting its hemopoietic properties.

The action of ultra-violet light in relieving milk anemia is not altogether clear. We know that wave lengths of light in the 300 uu to 680 uu range are capable of doing three things:

1. Sayre (17) has shown that these rays only are capable of producing chlorophyll.

2. In the presence of ergosterol these rays will produce vitamin D.

3. And as shown by Osata and Tanaka (7), Furniss (8), and Foster (9), these same rays will relieve milk anemia.

The action of halibut liver oil can perhaps better be interpreted when we recall that Simmonds, Becker, and McCollum (18) state that liver fats contain vitamin E in considerable amounts and also much iron. These authors claim that vitamin E in some way is hooked up with iron assimilation. They showed that ferrous sulphate alone in amounts as small as .2% in the food was harmful to rats, whereas, ferric citrate or the addition of wheat germ oil to the ferrous sulphate relieved the condition.

#### CONCLUSION

1. Plant pigments such as the chlorophylls, the carotins, or possibly the xanthophylls apparently are factors necessary for hemopoiesis in rats suffering from milk anemia.

2. Other factors that will relieve milk anemia are:

- a. Milk from cows that are on a specified green pasture diet.
- b. Halibut liver oil.
- c. Ultra-violet light irradiation.

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# THE EMBRYOLOGY OF THE WHITEFISH, *COREGONUS CLUPEAFORMIS* (MITCHILL)

## PART I

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### INTRODUCTION

The importance of the lake whitefish as a food fish has long been recognized, and the recent decline in its population in the Great Lakes is cause for serious concern. Its artificial propagation in state and federal hatcheries has been conducted on a large scale for more than fifty years. Several investigators, Couch ('23), Leach ('23), Van Oosten ('23), Mellen ('23), Koelz ('27, '31), Wickliff ('29), Hart ('30, '31), have made studies on the rate of growth, the age at sexual maturity, breeding and food habits, migrations, and hatchery methods, of this species. However, the literature dealing with the embryology of the Whitefish is confined to two series of microphotographs of the eggs undergoing cleavage, by Leach ('23), and by Wickliff ('28), and to a short description of the unfertilized egg and cleavage stages by Mrs. Fish ('29), whose paper deals primarily with the early life history subsequent to hatching. The present series of papers, of which this is the first number, represents a general survey of the embryology of this species, from fertilization until hatching. This first paper traces the major events of segmentation and germ-layer formation and general development up through the closure of the blastopore. The later embryology and development of each of the organ systems will be treated in subsequent papers. Such a preliminary survey has been made with the hope that it will serve as a basis for further study, and that it will also yield information useful in attacking various hatchery problems relative to whitefish propagation.

### MATERIALS

The eggs of *C. clupearformis* have a prolonged period of incubation, usually extending from the middle of November to the first week in April. Such an extended period permits the

collection of large series of eggs in closely graduated stages. During the winter of 1926-'27, a series of 803 stages was collected at the Ohio State Fish Hatchery at Put-in Bay, under the direction of Mr. E. L. Wickliff, Assistant Chief of the State of Ohio Division of Conservation. The eggs were taken at four hour intervals, day and night from one day after fertilization, November 21, 1926, until hatching time, April 5, 1927, a total of 134 days, 16 hours. Temperature readings were made at 8 A. M. and 4 P. M. daily during this period, using a Fahrenheit thermometer sensitive to fluctuations of one degree. This series is the basis for the present study, and it is now in the possession of the Department of Anatomy of the Ohio State University. The author wishes to express his appreciation to the State Department of Conservation and to the Anatomy Department for the use of this material and to Dr. Ralph A. Knouff for his constructive suggestions and criticisms of this study.

For purposes of a preliminary survey, every sixteenth stage of the eight hundred was studied, with additional ones in the early stages, making a series of fifty-five units. Those involving early cleavage, germ ring formation, the primitive streak, the formation and closure of the blastopore and the differentiation of the primary germ layers are described from surface views of whole mounts, and from serial sections, in the present paper.

Organogenesis from this point to hatching will be discussed in papers II and III of this series. This later development is shown by reconstruction drawings, which were built up from serial sections. These reconstructions indicate the general development of the brain, sense organs, cranial nerves, notochord, somites, pronephric tubules, the gut, branchial pouches and the heart.

#### METHODS

All of the eggs were fixed at the time of collection in Bouin's solution. When removed from this, the shell was tough and could easily be removed with needles. The yolk was fairly brittle, yet not so hard but that it could be sectioned satisfactorily. For most of the series, the sections were stained with iron-alum haematoxylin, and counter stained with eosin. A few embryos were stained *en toto* in Mayer's acid carmine. Greater differentiation was secured with the former method when the sections were allowed to remain in the mordant, but

not in the oven, overnight and from 24 to 48 hours in the haemotoxylin. The sections were cut ten microns thick and mounted by the water-albumen method.

For the preparation of whole mounts, the embryo was first picked off the yolk with fine needles. It was then cleared in cedar-wood oil, stained *en toto* with acid carmine, and mounted in balsam. Some of the mounts were simply cleared and not stained. In some respects, these served better for study than the stained embryos.

A vertical microprojecting apparatus calibrated to 100 diameters was used in making the reconstruction drawings of the later stages. Since the sections were cut ten microns thick, each section was represented by one millimeter on the drawing. The outline of the entire embryo of the stage to be reconstructed was first made from the whole mount of that stage. After the angle at which the sections had been cut was determined and the base line drawn on graph paper, then the image of a section thrown by the microprojector was transposed to the graph paper by using a pair of dividers to mark out the limits of the part being reconstructed. Every fifth section was thus transposed and these sections form the basis for the drawings made at 100 diameters. The magnification of the finished drawing is indicated by the size of scale beneath it. By this method, the embryo may be reconstructed on any desired plane, parallel to the antero-posterior axis of the body.

#### THE DESIGNATION OF STAGES

All of the eggs in this series were taken from the same incubation jar at the state fish hatchery. They had all been fertilized at the same time and subjected to the same temperatures and oxygen content throughout the incubation period. Any wide variation in temperature to which eggs of the same age had been subjected would probably result in marked fluctuations in the relative development of consecutive stages. However, no marked breaks or gaps in the series have been discovered. It is assumed therefore that all normal eggs had developed at approximately the same rate.

With temperatures of the lake in midwinter fluctuating about a mean of 33° F., whitefish in the state fish hatchery at Put-in-Bay have over a period of years had an incubation period of from 120 to 140 days (Leach, '23, Wickliff, '28). However, some embryos in the series described by Mrs. Fish

('29) reached the hatching stage on the 61st day. No temperatures were given for this series. Obviously, different series cannot be compared on the basis of time alone.

There are other bases however that may be used. Wallich ('00) designated the age of fish embryos by thermal units. By a thermal unit (t. u.) is meant a temperature of 1° F. above 32 degrees for a period of 24 hours. A mean temperature of 36° F. for one day yields 4 thermal units. Thus, when the incubation period for any series or any particular stage in that series is given in days, and the mean daily temperatures are known, the thermal units may be readily calculated by simple addition. The thermal unit then expresses the age of an embryo as the sum of both time and temperature. Embryos in different series whose ages in thermal units are the same would be comparable. For example, embryos incubated for 131 days at  $34\frac{1}{2}^{\circ}$  F. would have been subjected to 325 thermal units and they would be the same age on this basis as other embryos incubated for only 65 days at a mean temperature of 47 degrees. Assuming that this relationship between time and temperature holds within certain limits the thermal unit then may be used as a basis for making comparisons between embryos of different series.

The age in thermal units is given for every stage of whitefish embryos described in this series, together with the age in days. For post-cleavage stages, the length of the embryo and the number of somites are also designated. Thus there are four means of denoting the various stages in this series which may serve in making subsequent comparisons.

In the drawings, figure numbers correspond to the serial stage number from which they are taken.

#### DESCRIPTION OF EARLY CLEAVAGE STAGES THE UNFERTILIZED EGG

The unfertilized whitefish egg is approximately 3 mm. in diameter. (See Fig. 1a, Plate I.) It is round, almost transparent when alive, and free to turn in the perivitelline space beneath the shell. The shell is smooth, tough in texture, and is held turgid by the enclosed perivitelline fluid. The perivitelline space is less evident in unfertilized eggs than in eggs subsequent to fertilization. There is a collection of many oil globules at the animal pole of the egg. These are conspicuous

during the early segmentation stages, and underlie the developing germinal disc.

Notwithstanding the fact that a micropyle has been described for the eggs of the salmon (Doyere, '50), for the trout (Henneguy, '88), the carp, the pike, and for various other teleosts, I have failed to discover any indication of such a structure in the whitefish egg.

A thin layer of protoplasm of uniform thickness completely surrounds the yolk.

#### EARLY SEGMENTATION STAGES

*Four-celled Stage.*—Since the fixation of eggs as originally collected did not begin until twenty-four hours after fertilization, the events concerned with fertilization and the early cleavage cannot be described from this material. Mr. Wickliff, in the fall of 1927, however, secured eggs from the same source and under similar conditions, taken three hours after fertilization. These eggs were in the four-celled stage. (See Fig. 1b, Pl. I.) Judging from what is known in other species, there must have occurred a "streaming of protoplasm" toward the animal pole, for there is present in these eggs at that pole a rounded disc of protoplasm, lenticular in character. This disc of protoplasm tapers off rapidly at its edge, and continues over the surface of the yolk in an extremely thin layer. The first two cleavage planes are meridional and at right angles to each other. They cut deeply into the blastodisc but do not extend into the yolk.

*Eight-celled Stage.*—Stage No. 1, O. S. U. series. Incubation period: 1 day; 8 t. u. (See Fig. 1c, Pl. I.) In the egg that is figured, the blastodisc is somewhat longer than broad, with the eight or more blastomeres arranged roughly as four pairs, one behind the other. In an egg of this pattern, the first cleavage furrow must have been transverse to the long axis of the figure and through its center. The second cleavage furrow would then be at right angles to the first, along the antero-posterior plane. In the rounded blastodisc of the four-celled stage as figured, however, no antero-posterior lengthening can be distinguished. Since the first eggs of the series have already undergone these first two divisions, any attempts to identify the first cleavage planes with the antero-posterior plane of the embryo must be reserved for later study on living material. With regard to the third division, in

Fig. 1c, there must have been two transverse furrows, one through each pair of the first four cells, which by subsequent growth have produced an elongated blastodisc.

The serial sections of this stage were cut transversely, each section passing through two blastomeres. These cells are separated by a very fine membrane which extends deeply into the blastodisc, almost to the yolk. At the periphery of the blastodisc, the blastomeres continue into a progressively thinner layer of superficial protoplasm, which extends over the yolk. The zone of transition between the edge of the blastodisc and the superficial layer of protoplasm over the yolk constitutes the early periblastic ridge as described for *Serranus* by Wilson. The astral rays of the mitotic figures are very conspicuous, extending nearly to the boundaries of the cell. All eight cells are actively undergoing mitosis. The planes of the spindles in various cells which are in the metaphase condition indicate that the succeeding or fourth cleavage furrow will be parallel to the second, as described above, and at right angles to the third. This will produce four more or less distinct rows of cells and increase the breadth of the blastodisc, tending to restore its rounded outline, as in Fig. 4, Pl. I.

All eight-celled blastodiscs are not elongated as described above, although probably about three out of every four eggs at this stage show this pattern. Some were observed in which the blastodisc was distinctly circular and the cells were disposed symmetrically about a central point. In these, it is assumed that the first two furrows had been meridional and at right angles to each other, but the third cleavage furrow was completely circular and located midway between the center and the periphery of the blastodisc. This tendency of the third furrow to be circular is seen with all its modifications. Indeed, the third cleavage furrow in Fig. 1c, separating the third and fourth pairs of cells describes an arc of such a circle. It is well known that such variations in cleavage patterns are determined by varying rates of growth of the cells and by the relative pressures which they mutually exert upon one another. In eggs in which the cells are concentrically disposed, the fourth cleavage furrow is apparently meridional. The resulting cleavage pattern accompanied by some irregular growth of the cells is illustrated by Fig. 2, Pl. I.

In succeeding stages, the bilaterality of the blastodisc is no longer apparent. Fig. 3, Pl. I, is approaching the 32-celled

condition, and the blastodisc shows a decided tendency to become rounded up. By Stage No. 8, the blastodisc is completely rounded.

*Stage No. 8.* O. S. U. series—Incubation period, 2 days, 4 hours, 15 t. u. Transverse sections through this stage (see Fig. 8, Pl. II) reveal that, while the cells of the blastoderm are comparatively large, they have been reduced through cleavage to about one-fourth the diameter of cells of Stage No. 1. The blastodisc is four cells deep through its center but shallower at its margins. The cells at the surface are slightly broader than deep and closely joined at their edges, representing the initial stage in the formation of the epidermic stratum. The deeper lying cells are loosely arranged with spaces between them in the central portion of the blastodisc. These scattered spaces represent the segmentation cavity of a type similar to that described by Kopsch ('04) for the trout, and differs from the single continuous ventral one as described by Wilson for the sea bass. The early periblastic ridge at the margin of the blastodisc is prominent. The marginal blastomeres which form the ridge are prolonged into the protoplasm covering the yolk, to form the central periblast. The latter is an extremely thin layer of protoplasm lying immediately beneath the blastodisc. It is not separated from it by the segmentation cavity as shown in Wilson's figures 17 and 18 of *Serranus*. The yolk mass underlying the central periblast at this stage contains many scattered, irregularly shaped darkly pigmented bodies or granules which may constitute a syncytium of yolk nuclei, but more probably they are simply yolk granules. These are not to be confused with the syncytium of nuclei formed later in the central periblast from cells migrating inward from the periblastic ridge.

*Stage No. 16.* O. S. U. series—Incubation period 3 days, 12 hours, 30 t. u. The blastodisc is somewhat more prominently raised up on the yolk, and the outlines of the individual blastomeres are indistinct on the surface, owing to rapid cell division. Transverse sections of this stage, (Fig. 16, Pl. II) show the blastomeres reduced to about one-fourth their former diameter in Stage No. 8. They form a blastoderm of from eight to ten cells deep. The spaces of the segmentation cavity between cells are less conspicuous. The epidermic stratum which was forming in Stage No. 8 is clearly defined as a superficial layer of somewhat flattened cells. This stage corresponds closely to

that figured by Kopsch at the end of segmentation in the trout.

*Stage No. 32.* O. S. U. series—Incubation period, 6 days 4 hours, 42 t. u. *The formation of the germ ring and subgerminal cavity.* The egg is rapidly approaching the end of the segmentation phase of its development. Many more cells are now shown in a single cross section than in previous stages, there being as many as two hundred in sections through the center of the blastoderm. The cells are correspondingly smaller in diameter. Evidently segmentation is occurring rapidly. The blastoderm spreads out over the yolk surface more than in earlier stages, and accordingly it is thinner, being only from six to eight cells deep. The epidermic stratum is a clearly differentiated layer of cells at this stage.

The periblastic wall contains clusters of nuclei of cells which have probably migrated into it from the margin of the blastoderm and subsequently lost their cell walls, in the manner described by Wilson, pp. 216–217, for *Serranus*. These nuclei have reached the center of the periblast as indicated by their presence in that region. The central periblast is now a syncytium of scattered nuclei which continues uninterruptedly into the periblastic wall and the cortical protoplasm over the yolk. The early periblastic ridge has largely disappeared. The marginal cells of the blastoderm lying above the periblast are closely packed together to form a wreath-shaped thickening, the germ ring, which is clearly seen from surface views of whole mounts. (see Fig. 32, Pl. I). The blastoderm has become greatly arched over the curvature of the egg.

As a result, a single continuous segmentation or subgerminal cavity lies prominently between the central periblast and the overlying blastomeres, to one side of the center and just within the germ ring. This segmentation cavity is apparently formed here as a larger space than in the previous stage, simply as the result of the crowding of the cells at the periphery of the blastoderm. It is probably confluent with the smaller spaces scattered elsewhere between the cells of the cross section. If this be true, the isolated spaces in cross-sections of earlier stages may actually be confluent and thus be regarded as essentially homologous to this single continuous subgerminal cavity which arises at this stage. As the cells of the blastoderm are reduced in size through repeated divisions and crowded together by the overarching of the blastoderm, the spaces

between them are thereby diminished. These spaces are finally reduced to the vanishing point in cross-sections of the next stage, No. 48. The sole remaining space is a typical sub-germinal cavity.

*Stage No. 48*—Incubation period, 8 days, 20 hours; 60 t. u.

*The growth of the blastoderm; the primitive entoderm*—The growth of the blastoderm around the yolk continues rapidly after the completion of the germ ring in the previous stage. In the present stage, (see Fig. 48, Pl. I), the blastoderm envelops approximately one-third the yolk, and the germ ring is plainly visible at its periphery. The subgerminal cavity appears from the surface view as a translucent, circular area within the cap of cells. In cross-sections, this cavity extends broadly beneath the blastoderm. It has clearly defined limits which extend to the marginal cells of the germ ring from within. The blastoderm is more elevated above the periblast than in *Serranus*, but the marginal cells of the germ ring are similar to those in Wilson's figures 46 and 47, Pl. XCIV. The subgerminal cavity is slightly eccentric, due to the rapid proliferation of cells on one side of the germ ring to form a deeper lying mass of undifferentiated cells, the embryonic bud. (See Fig. 48, Pl. II). In this area the cells are compact and the blastodisc is approximately twice as thick as elsewhere. The embryonic bud is destined to give rise to the embryonic shield and its posterior margin will constitute the dorsal lip of the future blastopore.

A tongue of primitive entoderm extends anteriorly from the embryonic bud toward the center of the blastoderm. At this stage, it reaches almost to that point. The periblastic layer has become fully developed, and retains the features described in the previous stage. Throughout the remainder of the embryonic period, the periblast remains unmodified, as the covering of the yolk beneath the embryo.

*Stage No. 64*—Incubation period, 11 days, 12 hours, 82 t. u. The blastoderm is flattened out as a sheet of cells enveloping the upper half of the yolk sphere, with the germ ring lying in the equatorial plane. (See Fig. 64, Pl. I). In some whole mounts of this stage, the blastoderm is translucent, at least in the extra-embryonic portions and the yolk surface beneath is clearly visible. While the embryonic shield is hardly visible from surface views, cross-sections show that it is definitely established. In the posterior end of the shield,

an undifferentiated caudal mass of cells arises abruptly, with its thickest portion in the axial line. Just anterior to the caudal mass, the shield extends laterally to end abruptly at its margins. In cross-sections at this level, (see Fig. 64, Pl. II), beneath the epidermic stratum lies the ectodermal layer, several cells deep, underlaid by a two-rowed cell layer of primitive entoderm. The entoderm extends forward as a tongue of cells, as described for the previous stage, No. 48, but now underlies the entire shield, thus obliterating the subgerminal cavity. In the central axial portion, the entoderm from either side fuses into an undifferentiated line of cells, which represents the first step in the formation of the notochord. As the anterior end of the embryonic shield, the two layers of the entoderm lose their identity and appear as a single layer which fuses with the overlying ectoderm, a condition which represents the first step in the formation of what Wilson termed the neurenteric streak. (See Wilson, Fig. 52).

*Stage No. 80*—Incubation period, 14 days, 4 hours, 93 t. u. The embryonic shield becomes clearly visible on the whole mount at about Stage 72, but is figured for the first time in the drawing of this stage, Fig. 80, Pl. I. The somewhat triangular area represents the thickened embryonic portion of the blastoderm, in contrast with the lateral extra-embryonic portion which extends as a thin sheet of blastoderm over the curvature of the yolk to end in the germ ring at its margins. The bluntly rounded apex of the shield has extended forward from the condition described in Stage 64 and now clearly marks off the anterior end of the embryo.

The so-called neurenteric streak, which was beginning to form in the previous stage, is now clearly visible from the surface view, as a median longitudinal opaque area which extends from the anterior end of the embryonic shield backward to the notochord. It marks the location of the neural chord in the head end of the embryo.

From its incipient condition in Stage 64, the notochordal area has grown forward from the caudal mass and occupies the posterior third of the embryonic area. It appears in surface views of whole mounts as a light streak in the axial line. It is still an undifferentiated cell mass, fused laterally with the entoderm.

The extra-embryonic portion of the blastoderm extends laterally and anteriorly beyond the embryonic shield to the

germ ring as mentioned above, and it now encloses two-thirds of the yolk. In this extension of the blastoderm, the direction of growth is difficult to determine. There are no definitely placed oil globules as there are in *Serranus*, by which to judge the relative position of the germ ring. In *Serranus*, in *Salmo*, and in various other teleosts, it has been shown that the position of the caudal mass and hence that portion of the germ ring which constitutes the dorsal lip of the blastopore is relatively fixed. In such cases, extension takes place by way of the anterior margin of the germ ring growing around the yolk. However, in *Hemichromis*, in which the egg is oblong, McEwen ('30) describes also a backward growth of the dorsal lip of the blastopore. Thus all portions of the germ ring take part in the closure of the blastopore by their migration toward the point of closure. In spite of Wilson's statement to the contrary, p. 222, the posterior end of the sea bass embryo in his Fig. 38, Pl. XCII, is somewhat closer to the oil globule than it is in his Fig. 36 of an earlier stage. The difference is not marked however. Thus there is some backward growth of the dorsal lip of the blastopore, although it is slight in comparison to the migration of the anterior margin of the germ ring over more than half the yolk surface to finally meet the dorsal lip at the point of closure. In the Whitefish, the closure of the blastopore occurs in much the same way as in *Serranus*, involving mostly epiboly of the anterior or ventral lip, supplemented by some concrescence and by a slight backward growth of the dorsal lip.

*Stage No. 96*—Incubation period, 16 days, 20 hours, 97 t. u. This stage is marked by the further growth of the blastoderm around the yolk, advancing to a *large yolk plug stage*. The embryonic shield has increased to 2.0 mm. in length. This increase in length is due partly at least to a slight backward extension brought about by a concrescence of the lateral lips of the blastopore. The line of this concrescence would correspond to the primitive streak of other forms and is marked by a thickened mass of cells referred to in Fig. 96b., Pl. II, as the caudal mass. Kupffer's vesicle is seen for the first time in this stage. It appears on the floor of the caudal mass. Its walls are formed by a single layer of regularly arranged cells. Just anterior to this vesicle, the notochord arises, possessing a distinct outline and a compact shape. Its anterior end extends two-thirds the distance from the caudal mass to the anterior

end of the embryo. The lateral mesodermal plates are now readily distinguished from the surface ectoderm dorsally, from the notochordal area medially and from the entodermal cells ventrally (See Fig. 96c. Pl. II). The ectoderm is now greatly thickened over the entire embryonic shield, as compared to the extra-embryonic portion. In the anterior end of the embryonic area, this ectodermal thickening is very marked, forming the neural keel. Above it, dorsally, a shallow median neural furrow appears, into which dips the epidermic stratum. This furrow is transitory, and disappears in a slightly later stage, No. 112. At this level the primitive entoderm forms a single cell layer beneath the neural keel.

*Stage No. 112*—Incubation period, 19 days, 12 hours, 103 t. u. Length of embryo: 2.32 mm. (See Fig. 112, Pl. I and II). By this stage, the neural keel has undergone a marked downward growth into the yolk mass. As it continues to thicken and grow deeper, the lateral portions of the neural keel grow thinner, as the result, according to Wilson, of cell migration. Thus in surface views the so-called neurenteric streak of the embryo projects anteriorly from the original dorsal lip of the blastopore as a long narrow opaque area on the surface of the yolk, of almost uniform width throughout its length, but with greater depth at the anterior end. The neural furrow, mentioned in the previous stage, is shown in the surface view here, but it disappears with this stage. It fades out progressively from behind forward. The cells of the neural keel are the same in appearance throughout, not yet being stratified nor differentiated. The optic primordia make their first appearance at this time, as solid cell masses.

The outline of the notochord is visible from the surface view. Its anterior end extends two-thirds the distance from the caudal mass to the anterior end of the embryo. In the posterior region, its cells are rounded up and may be easily distinguished from the nerve cord, the mesodermal masses, but somewhat less distinctly from the entoderm. Farther forward, however, it is progressively less differentiated. The mesodermal plates, described in Stage 96 as having separated from the adjacent layers, are now divided into two parts: the one more mesial which later forms the dorsal mesodermal plates; and the outer part, which later forms the lateral mesoderm, the intermediate cell mass and its derivatives, and the Wolffian ducts. (See Fig. 112, Pl. II; also, Swaen and Brachet,

Fig. 66, Vol. 16, '00). In the middle region of the embryo; the dorsal mesoderm is for the first time composed of a solid rosette of cells which represents the somite. There are apparently three pairs of somites present at this stage. The lateral mesoderm is likewise a solid mass of cells. On its mesial border is a single line of cells which later splits off from the remainder of the mass to form the intermediate cell mass. At the level of the somites, the entoderm lies over the periblast as an unfolded sheet of cells, one layer thick. This stage is distinguished by the *narrow yolk plug*. The blastopore is almost closed at this time.

*Stage No. 128*—Incubation period, 22 days, 4 hours; 108 t. u. Total length of embryo: 2.96 mm.; eleven pairs of somites; closure of the blastopore. In contrast to the previously described stage, very marked cephalization has occurred at this time, as seen in both the surface view drawing, Fig. 128, Pl. I, and in the reconstruction drawing of this stage (Fig. 128, Pl. II). Three primary cerebral vesicles have developed. The neural keel in the head region has continued its downward growth and lies half imbedded in the yolk. Its depth in the brain-forming region is at least twice that of its depth in the middle portion of the spinal cord region of the embryo. There are no cerebral ventricles present at this stage however, and the optic outgrowths are still solid cell masses. The cells of the neural keel are no longer indifferently placed, but are becoming rearranged into two parallel rows which separate in Stage 144, to form the cavity of the neural canal. This rearrangement of cells takes place first in the prosencephalon and continues backward to the middle region of the neural cord. The optic anlagen which appeared in Stage 112 have greatly enlarged, and in the reconstruction drawing are shown as projecting prominently from the sides of the prosencephalon. They are now separated externally from the brain by a fissure which appeared in Stage 120 and which now extends from above downwards and from behind forwards, leaving only the ventral portion connected with the prosencephalon. This connection is the optic stalk.

Immediately posterior to the anlage of the eye is a mass of head mesoderm, of mesenchymatous appearance. While it appears here as a distinct mass, its later disposition has not been thoroughly traced. There is but little evidence of the existence later of head somites, and none of segmentally arranged

head cavities. A wing of lateral mesoderm extends along the sides of the body from the anterior end of the paired somites at the level of the rhombencephalon forward to the middle portion of the head region. It spreads out laterally on the yolk surface, but since the keel sinks so deeply into the yolk, the mesoderm appears high on the side of the head. A longitudinal furrow appears in this same region on the dorso-lateral surface of the head at the angle between the neural keel and lateral mesoderm. It is probably the so-called sensory furrow described by Wilson in *Serranus*, and as such is the anlagen of the auditory pit and lateral line sense organs.

The notochord anterior to the caudal mass is two or three cells deep. Its cells are interlocked and are approaching a period when their vacuolation begins. Anteriorly the notochord is clearly separated from adjacent areas. It extends with the flattened layer of entoderm beneath it forward to the level of the midbrain. This position is retained hereafter.

Eleven pairs of mesodermal somites are present, as shown in the drawing. Kupffer's vesicle, which appeared in Stage 96, has now reached its maximum development in the floor of the caudal mass, and from this time on, it begins to diminish in size. The blastopore is completely closed over on the surface, and its position is marked by a narrow indentation or furrow in the tail region.

#### SUMMARY

From the foregoing descriptions, it is seen that the Whitefish, in its early development up to the closure of the blastopore, is typically teleostean. The 3 mm. egg with its capsule, perivitelline space, and the concentration of oil globules at the animal pole agrees closely with eggs of other species, although a micropyle is apparently absent. The formation of the blastodisc and the cleavage of the blastomeres follows closely the pattern described by other writers for the trout, the sea bass, and other species, and may be regarded as typical of telolecithal eggs. The early segmentation cavity, by virtue of the fact that it is interspersed between scattered cells of the blastoderm, resembles that of the trout, but differs from that of *Serranus*. It may probably be regarded as a characteristic of the *Isospondyli*.

The growth of the blastoderm over the yolk, the formation of the germ ring, the periblast and the primitive entoderm,

the delineation of the embryonic shield and within it, the differentiation of the three primary germ layers, all proceed in much the same manner as previously described for other Teleosts.

However, the relative degree of development attained by the whitefish at the time of the closure of the blastopore is of special interest. In this series, this event has occurred by Stage 128, when these eggs have been incubated for 22 days and have been subjected to 108 thermal units. In terms of days, these eggs have completed just  $\frac{1}{4}$  of their incubation period, but  $\frac{1}{4}$  of the incubation period in terms of thermal units. The higher proportion of the latter is due to the fact that, during the first part of the incubation period, the temperature of the lake water is comparatively high, and the ratio of thermal units to days is consequently higher than later in the season, when the daily temperatures descend to around 33° F. It is seen then that the blastopore closes within the first sixth of the incubation period in point of time and within the first third of this total period on the basis of both time and temperature (thermal units). At this stage, the embryo is clearly outlined, lying in a straight line over the curvature of the egg, with a length of about 3 mm., which is just one-fourth its hatching length. Within the body of the embryo, all three primary germ layers have undergone considerable differentiation. Derived from the ectoderm, the three primary brain lobes are distinct, and the neural keel lies deeply imbedded in the yolk. The optic primordia are now borne on broad optic stalks. The mesoderm has given rise to a mass of head mesoderm, to the notochord which now extends forward its full length to end beneath the midbrain, and to eleven pairs of somites, or about  $\frac{1}{4}$  of the hatching number. Kupffers' vesicle has reached its maximum development. The entoderm is undergoing rapid changes, preparatory to the development of branchial pouches.

When compared with other species of teleosts whose embryology has been studied, it is seen from the above items that the whitefish is notably well differentiated at the closure of the blastopore.

It now remains for later papers of this series to outline the embryology of the whitefish during the remainder of the incubation period, subsequent to the closure of the blastopore.

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## LIST OF ABBREVIATIONS USED IN THE FOLLOWING PLATES

- |                                    |                               |
|------------------------------------|-------------------------------|
| b. d.—blastoderm.                  | Mesen.—mesencephalon.         |
| Bl.—blastopore.                    | n. f.—neural furrow.          |
| c. m.—caudal mass.                 | noto.—notochord.              |
| c. p.—central periblast.           | n. s.—neurenteric streak.     |
| d. mes.—dorsal mesodermal plate.   | o. g.—oil globule.            |
| ecto.—ectoderm.                    | op. prim.—optic primordium.   |
| e. e. s.—edge of embryonic shield. | op. st.—optic stalk.          |
| em. bd.—embryonic bud.             | P.—periblast.                 |
| ento.—entoderm.                    | pr. ento.—primitive entoderm. |
| ep.—epiblast.                      | Prosen.—prosencephalon.       |
| e. s.—egg shell or membrane.       | p. v. s.—perivitelline space. |
| e. p. r.—early periblastic ridge.  | Rhomb.—rhombencephalon.       |
| ep. str.—epidermic stratum.        | s. c.—segmentation cavity.    |
| g. r.—germ ring.                   | s. f.—sensory furrow.         |
| hd. mes.—head mesodermal mass.     | s. g. c.—subgerminal cavity.  |
| i. c. m.—intermediate cell mass.   | som. XI—somite eleven.        |
| K. v.—Kupffer's vesicle.           | y.—yolk.                      |
| lat. mes.—lateral mesoderm.        | y. g.—yolk granule.           |
| mes.—mesoderm.                     | y. m.—yolk mass.              |

## EXPLANATION OF PLATES

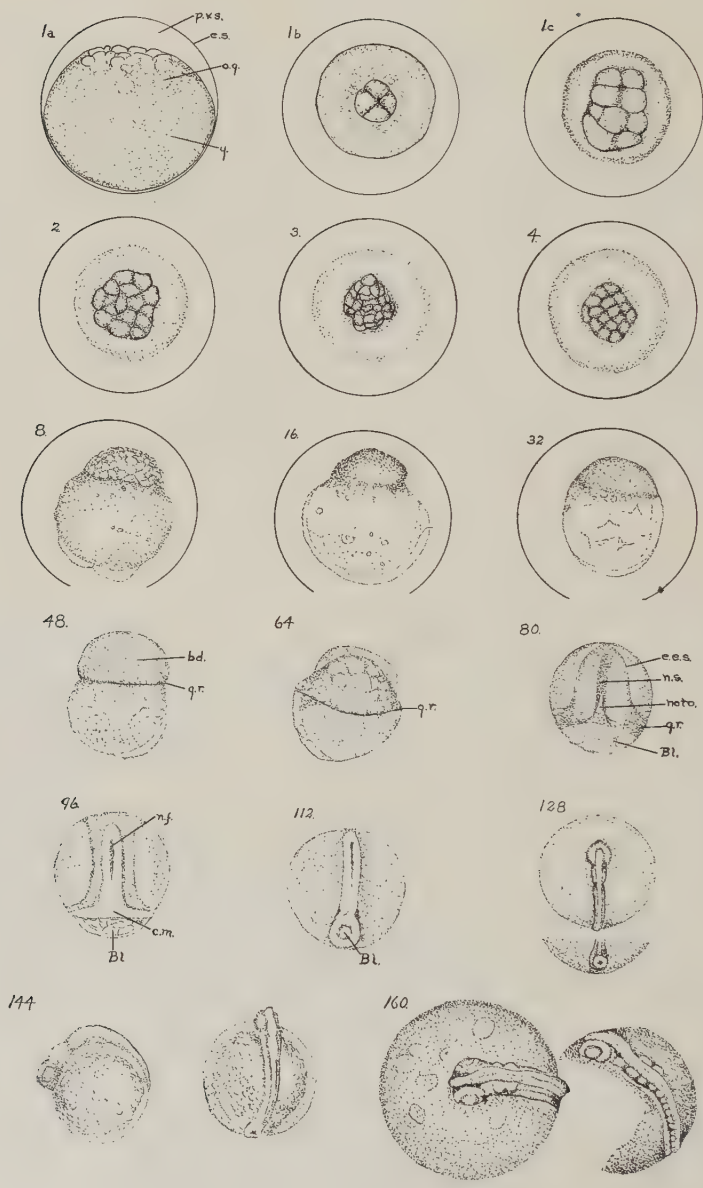
(Figure numbers correspond to the serial stage number from which they are taken.)

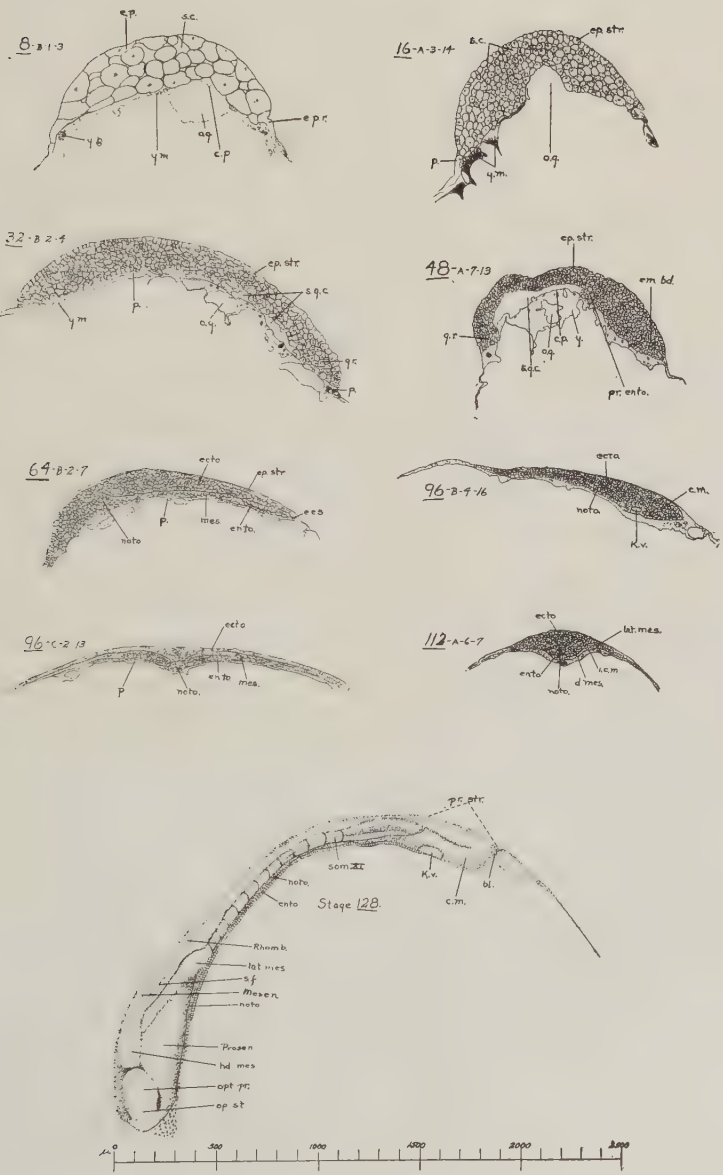
## PLATE I

- Fig. 1a. Unfertilized egg, with animal pole uppermost.  
Fig. 1b. Four-celled stage, 3 hours after fertilization.  
Fig. 1c. Blastodisc of about 8 cells, from above.  
Figs. 2, 3, 4. Early segmentation stages, 16-32 cells.  
Figs. 8, 16, 32. Later segmentation stages.  
Figs. 48, 64. Formation of germ ring, and growth of blastoderm.  
Fig. 80. Showing embryonic shield, neurenteric streak, blastopore.  
Fig. 96. Large yolk plug stage, showing outlines of early embryo.  
Fig. 112. Narrow yolk plug stage.  
Fig. 128. Closure of the blastopore. Three primary brain lobes.  
Figs. 144, 160. Surface views of subsequent development.

## PLATE II

- Fig. 8. Cross-section through center of blastodisc of Stage 8. (Drawn from slide B, first row, third section of serial mounts in O. S. U. series. Similar code is used to designate drawings of sections of other stages.) Shows early segmentation cavity, and early periblastic ridge.  
Figs. 16, 32, 48. Cross-section of corresponding stages shown in Plate I, showing formation of subgerminal cavity.  
Fig. 64. Cross-section through one side of embryonic shield, showing an undifferentiated notochordal area in mid-ventral line.  
Fig. 96 B. Cross-section cut obliquely through dorsal lip of blastopore, showing Kupffer's vesicle, and the differentiation of notochordal tissue anterior to caudal mass.  
Fig. 96 C. Cross-section more anterior than 96 B. The primitive entodermal layers are definitely separated into single layers of mesoderm and entoderm.  
Fig. 112. Cross-section through dorsal mesodermal plate.  
Stage 128, Reconstruction drawing, showing embryo in natural position over curvature of the yolk. This stage marks the closure of the blastopore.





# DUPLICATE EVOLUTION OF PECULIAR PERIANTH STRUCTURES IN THE SEDGE FAMILY AND THE COMPOSITES

STUDIES IN DETERMINATE EVOLUTION, VIII<sup>1</sup>

JOHN H. SCHAFFNER

It is not at all surprising to find similarity of structures and parts in closely related forms. Such similarities are at present usually taken for granted because we know that segregative evolutionary movements, although they establish barriers beyond which no further evolution is possible, do not prevent progressive changes of a parallel nature in the segregated groups. Thus two related groups may evolve series of almost identical characters. In the past, such duplicate developments have often been described as examples of mimicry. But the old teleological hypothesis of mimicry, as developed by the followers of Darwin, is almost entirely a figment of a very vivid imagination and very commonly was based on the most ridiculous propositions and fancies. No one without a very enthusiastic credulity would at present attempt to maintain such fantastic explanations of biological phenomena except those to whom teleological theories are a sort of confession of faith handed down from a former generation of teleologists, who could not conceive of any biological structure except in terms of some special advantage or use which would preserve the individual in an unfortunate and cruel world, where tooth and claw, heat and cold, and the like determined the whole course and direction of evolution.

In the present paper is presented a series of remarkable, parallel developments from two groups of plants which are not only widely separated in relationship but exist in very different environments. The species of the sedge family represented are mostly hydrophytes, some growing as partially submerged aquatics and others in moist or wet habitats, while those of the composite series are nearly all mesophytes, some of them growing in quite dry soils. Both groups are far advanced along evolutionary lines and far removed from any past connecting links. The sedges are monocotyls with closed vascular

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<sup>1</sup>Papers from the Department of Botany, The Ohio State University, No. 334.

bundles, parallel-veined leaves, and trimerous, hypogynous flowers, while the composites are dicotyls with open vascular bundles, netted-veined leaves, and pentamerous, epigynous flowers.

The primitive type of flower of the sedges has a dicyclic, trimerous perianth. In the species of *Oreobolus* the perianth segments are all broad and resemble somewhat the sepals and petals of a *Juncus*. From this condition there is a gradual modification and reduction until in the extreme forms there is no vestige of a perianth left. In Figure 1 is represented a mature flower of *Fuirena hispida* Ell. The three petals are stalked and have broad blades with forwardly projecting barbs, but the sepals are reduced to bristles with backwardly projecting barbs. In the genus *Scirpus*, the perianth is reduced so much that all the segments, whether representing sepals or petals, are reduced to bristles. These bristles are attached to the base of the achene when it is shed. In some of the species the bristles have no barbs whatever, as in *Scirpus caespitosus* L. (Fig. 2). The plant is entirely indifferent in this respect. In *Scirpus cyperinus* (L.) Kunth. (Fig. 3), the bristles are also destitute of barbs, but a new factor causes them to be developed as long and flexible hairs, which are responsible for the plants common name "Wool-grass." Many of the higher species of *Scirpus* have developed barbs on the perianth bristles. In *Scirpus americanus* Pers. the perianth bristles have very prominent, retrorse barbs (Fig. 4). *Scirpus planifolius* Muhl. (Fig. 5) has outwardly projecting barbs on the perianth bristles. Thus of these four species of *Scirpus*, two are indifferent as to barbs, one has retrorse barbs and can thus hold on to things while the other has forwardly projecting barbs which prevent the bristles from being attached to objects. All three types of perianth bristles, non-barbed, forwardly barbed, and retrorsely barbed, are also found in species of *Rhynchospora* and *Eleocharis*, although in the latter genus the bristles are mostly retrorsely barbed. All types exist in the same ecological conditions and it is evident that the different types did not originate through the direct influence of the environment nor through a life and death struggle for existence in the environment. All are successful. Any teleological explanation would be a mere fairy tale.

Turning now to the composites which show similar developments, and which have been used extensively by teleological

biologists to prove their case, we find a strikingly parallel series in the genus, *Bidens*, only in this case the calyx alone is involved, the corolla continuing as a normal structure. *Bidens tereticaulis* D. C. (Fig. 14) has entirely smooth sepal awns corresponding to the bristles of *Scirpus caespitosus* L. It is also entirely indifferent as to whether it is to catch on to anything or not. But *Bidens frondosa* L. (Fig. 13) has prominently retrorsely barbed sepal awns which are able to catch on to the fur of various animals. Thus the seed may be carried far from the paternal acres and perhaps deposited in very sterile or unfavorable soil. Various other species of *Bidens* have these retrorsely barbed awns or bristles, one of the commonest being *Bidens bipinnata* L., the Spanish-needles. Now in *Bidens bidentoides* (Nutt.) Britt. (Fig. 12) the sepal awns are again outwardly barbed as in *Scirpus planifolius* Muhl.

It will be seen that in each of these two genera the awns or bristles have evolved all the possibilities in respect to the presence and position of barbs and the species of the several types are often found growing side by side in the same locality and in the same habitat, those of *Scirpus* in hydrophytic conditions, those of *Bidens* in ordinary mesophytic fields or waste places. There is neither an advantage nor a disadvantage in having barbs or in not having them, nor does it make any difference to the plant in its survival or in its ability to be distributed whether the barbs project forward or backward. All the multitude of articles and books which have dilated on the advantage to the species of being widely distributed through such means are based on imaginary presumptions. We might just as well presume that any plant was at a disadvantage in possessing special structures which would facilitate removal from its original favorable habitat. There are genera in both the Cyperaceae and in the Helianthaceae which have no special structures whatever for distribution which are among our most widely distributed plants. In *Cyperus* the perianth is entirely absent and the achene has no appendages whatever. In *Anthemis cotula* L. and *Chrysanthemum leucanthemum* L. the achenes have no pappus bristles nor any other kind of appendage, but just as in the case of various species of *Cyperus*, they are among the most widely dispersed species in the world. The notion developed in the past and for a time held as a fundamental principle of biology, written into almost every elementary text-book of botany and nature study, that these

special structures were evolved through a life and death struggle for existence or as a result of the direct influence of environment is highly irrational and is evidence of an extreme credulity in the scientists of the past generation.

As noted above, *Scirpus cyperinus* (L.) Kunth. has evolved its six perianth segments into long flexible threads. This change of perianth segments to long thread-like structures has been highly evolved in the genus, *Eriophorum*. The species of *Eriophorum* form a prominent orthogenetic series in this respect. In *Eriophorum alpinum* L. (Fig. 6) there are only the six original perianth segments in the flower, but these are greatly elongated. In Figure 6 the perianth hairs are represented one-half their comparative length. From this condition the various species represent a series in which the perianth cycle consists of a greater and greater number of pappus hairs until a very extreme condition is reached in *Eriophorum viridicarinatum* (Engelm.) Fern. which has about 70 pappus hairs (Fig. 7).

Passing from these bog plants to the dry land plants of the composites, one is again impressed by the remarkable similarity in the evolutionary development. Among numerous genera that might be taken to represent a condition corresponding to *Eriophorum alpinum* L., *Elephantopus tomentosus* L. shows a close parallel (Fig. 8). There are five sepal bristles, the petals not being affected as they are in *Eriophorum*. These bristles have flat bases but are very slender toward the top. In *Elephantopus spicatus* Aubl. (Figs. 9a, 9b), a Guatemalan plant, the pappus bristles have a very peculiar character in that each one has a characteristic double fold toward the outer end. This is one of those oddities which one finds when approaching the extreme limits of most of the higher phylogenetic series. That the Guatemalan climate or politics has nothing to do with this remarkable oddity is shown by the fact that *Elephantopus scaber* L., another Guatemalan species, has straight bristles like our own *Elephantopus tomentosus* L. and *Elephantopus carolinianus* Willd.

In some composites there is a double whorl of pappus scales. Thus in *Cymbia occidentalis* (Nutt.) Standley, a dry prairie plant, there are five flat scale-like sepals and five extra bristles at the angles, making an inner series and indicating that multiplication of the pappus units has begun (Fig. 10). This double series of broad scales and slender bristles simulates such

forms as *Fuirena hispida* Ell. In both the Helianthaceae and Cichoriaceae there are many series ending in numerous pappus bristles. The ultimate members of each series have no direct relation to each other but were evolved through a series of steps from more simple ancestral types. Figure 11 represents an achene of *Lactuca villosa* Jacq. whose numerous pappus bristles show an extreme evolution from the original and simple five sepals, as those of *Eriophorum viridicarinatum* (Engelm.) Fern. show an extreme development from the original six-parted perianth.

At present it is probably useless to speculate on the cause of the remarkable parallelism shown in the evolution of the pappus bristles of two groups so distant in relationship and so diverse in habitat as species of *Eriophorum* and the Cichoriaceae. It is sufficient to note the fact that such developments are very commonly the accompaniments of extreme reductions and attenuations in structures that were originally much more normal organ systems. There are many other extreme groups which show such structures. Very remarkable are the pappus developments in various species of *Eriocaulon* and *Lachnocaulon*, which genera are among the most extreme in the Liliales series, having heads of small flowers with involucre simulating closely the heads of many Compositales. In some species the sepals show some transformation into clusters of hairs but the most striking examples are represented by species like *Eriocaulon griseum* Koern. in which, in the carpellate flower, both the sepals and petals have been greatly reduced and transformed into numerous pappus bristles quite similar to those in *Eriophorum* and *Lactuca*. The three sepals in this species are, however, still distinct broad structures but with short hairs at the outer tips. In the closely related *Lachnocaulon anceps* (Walt.) Mor. the space representing the petal cycle is also occupied by copious, woolly hairs between the three sepals and the ovulary. In each of these genera a long orthogenetic series of more and more advanced developments in respect to pappus development is also in evidence.

Among the Valerianaceae, *Valeriana pauciflora* Mx. and *Valeriana edulis* Nutt. develop calyx pappus bristles much like some of their distant relatives in the Compositales and the same is true of *Scabiosa arvensis* L. among the Dipsacaceae. In the highest Pandanales, as in species of *Typha*, the extremely reduced carpellate flowers develop abundant long hairs on the

pedicels while their near relatives, the Sparganiaceae, considerably lower in the evolutionary series in nearly every respect, have small perianth segments and no bristles in or below the carpellate flowers. In a general sense the same is true in the higher grasses, where bristles and plumes are very prominent in such highly evolved tribes as the Agrostideae, Paniceae, and Andropogoneae. Among the extreme forms of the Paniceae, like species of *Chaetochloa*, and related genera, special bristles, some retrorsely barbed and some forwardly barbed and also giving orthogenetic series of greater and greater numbers of cortical bristles around the groups of spikelets, are very prominently developed but are not connected directly with the floral structures and so remain on the dead stalks after the fruits have been shed. In the Andropogoneae, the most extreme tribe of the grass family, bristles and large hairs are often very prominent features of the extremely reduced spikelets, giving rise to the popular names, beard-grass, wool-grass and plume-grass commonly applied to these plants.

All of these developments are to be regarded as the outcome of extreme evolutionary movements which have no relation to a supposed response to environment since they occur in the most diverse environments and circumstances, and in the most diverse morphological systems. Nor, as stated, do they have any relation to utility, for frequently they are so situated that they cannot become a part of the distributional mechanism. Even if they are a permanent part of the fruit and thus accomplish wide distribution through the agency of wind or animals, they are, nevertheless, not at all to be regarded in any special or teleological sense as being produced because of a special utility, since, as shown above, species without any devices whatever for distribution are just as successful and often more so and are able to be just as widely distributed as those which have the special structures as extreme over-adaptations.

These studies again show that even the so-called ecological adaptations may have no relation to special environments, that the most diverse structures occur in the same environment, and that the same structures evolve in very diverse environments. They indicate that evolution is kinetic, orthogenetic, and determinative, and that these remarkable progressions are conditioned by internal causes.



- Fig. 1. *Fuirena hispida* Ell. Mature flower with achene and six perianth segments, the sepals reduced and with retrorse barbs.  
 Fig. 2. Perianth segment of *Scirpus caespitosus* L., without barbs.  
 Fig. 3. Elongated, flexible perianth segment of *Scirpus cyperinus* (L.) Kunth.  
 Fig. 4. Retrorsely barbed perianth segment of *Scirpus americanus* Pers.  
 Fig. 5. Perianth segment of *Scirpus planifolius* Muhl. with outwardly projecting barbs.

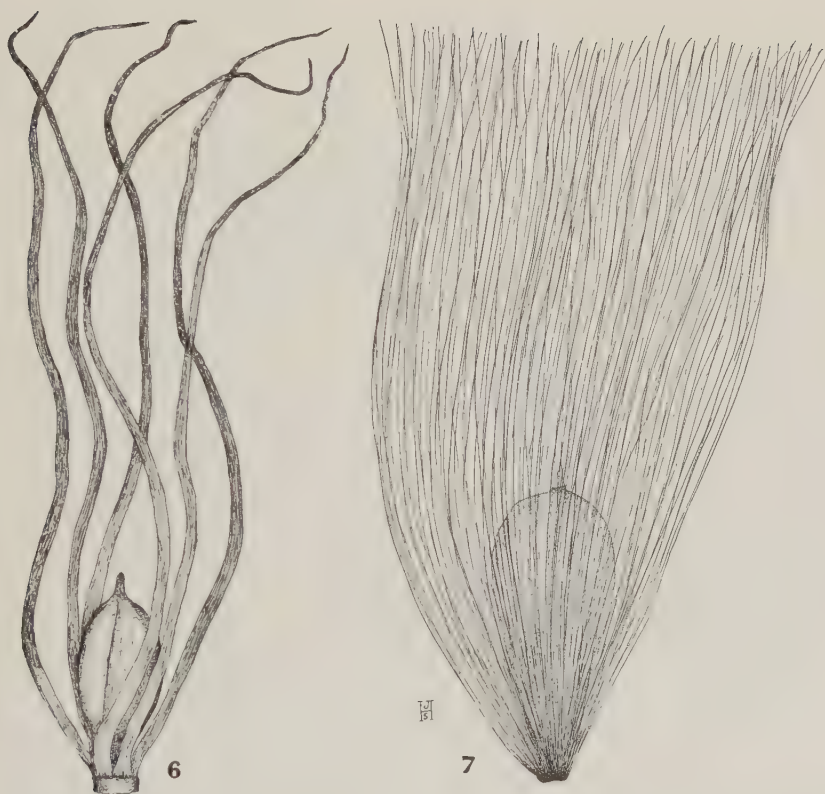
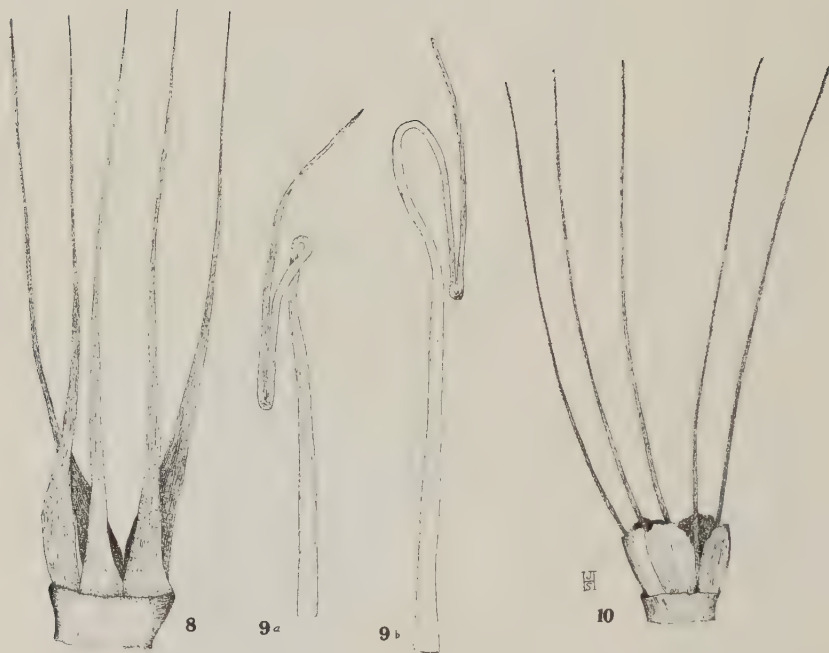


Fig. 6. Flower of *Eriophorum alpinum* L., with the six elongated perianth segments represented half the comparative length.

Fig. 7. Achene of *Eriophorum viridicarinatum* (Engelm.) Fern., showing the original six perianth segments replaced by about 70 slender bristles, which are represented one-half their comparative length.



- Fig. 8. Pappus of *Elephantopus tomentosus* L., showing the five elongated calyx segments.
- Figs. 9a, 9b. Pappus segments of *Elephantopus spicatus* Aubl., showing a peculiar double fold toward the outer end.
- Fig. 10. Double pappus of *Cymbia occidentalis* (Nutt.) Standley, showing five short flat scales and five long bristles.

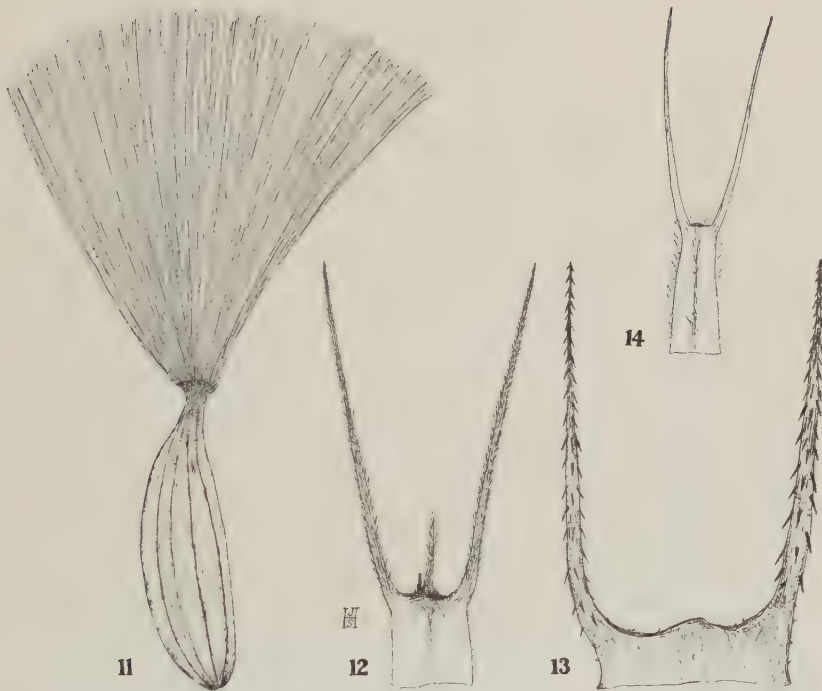


Fig. 11. Achene of *Lactuca villosa* Jacq., showing the very numerous pappus bristles.

Fig. 12. Outwardly barbed pappus awns of *Bidens lidentoides* (Nutt.) Britt.

Fig. 13. Retrorsely barbed pappus awns of *Bidens frondosa* L.

Fig. 14. Awns without barbs of *Bidens tereticaulis* DC.

## ADDITIONS TO NORTH AMERICAN FRESH- WATER BRYOZOA

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Two summers of intensive collecting for Bryozoa on and around twenty islands and localities in southwestern Lake Erie resulted in the addition of nine forms to the seven already known from Lake Erie and the addition of several forms to the North American list. At the present time there are approximately 21 species and varieties of freshwater Bryozoa known from North America—sixteen of which are represented in Lake Erie. Nine of the twenty islands from which collections were taken are Canadian possessions.

Specimens of *L. carteri* var. *typica* from Lake Erie were sent to the U. S. National Museum on March 6, 1934, and entered in their records as No. 128395.

I respectfully submit the following corrections to Dr. Dahlgren's account:

1. Carter had colonies as well as a statoblast from which to make his observations. He commented on the fact that this form resembled *Lophopus*, that the coenoecia exhibited movement and that the ectocyst was difficult to follow, etc. Carter, 1859, Ann. Mag. Nat. Hist., (3) III: 341.
2. Hyatt in 1866 recognized it as a new species and called it *Pectinatella Carteri* instead of *Lophodella carterii*. Hyatt, 1866, Proc. Essex Inst., vol. IV: 203 (Comm.).
3. Hyatt's designation as *P. Carteri* was still used in 1885. Jullien, 1885, "Monographie, etc.," Bull. Soc. Zool. France, X.
4. The genus *Lophopodella* (not *Lophodella*) into which *carteri* is now usually placed, was erected by Rousselet in 1904. Rousselet, 1904, Jour. Quek. Micr. Club, (2) IX: 45-56, April, 1904.
5. Oka in 1906 discussed *P. davenporti* (Zool. Rec. vol. XLV, 1908). This form is classed as another variety of *L. carteri*, var. *davenportii* (Hastings, 1929, Ann. Mag. Nat. Hist. (10) III: 305.

6. The citation "*Ulman* in 1907 from equatorial Africa" possibly refers to *Ulmer*, 1912, Wiss. Ergebnisse d. Deutsch Zentral-Afrika Exp. 1907-8, Band IV: 285-290.

TABLE I

THE DISTRIBUTION OF THOSE BRYOZOA WHICH WERE COLLECTED IN LAKE ERIE

| FORM                                | LAKE ERIE      |                   | NORTH AMERICA  |                   | WORLD DISTRIBUTION                                      |
|-------------------------------------|----------------|-------------------|----------------|-------------------|---------------------------------------------------------|
|                                     | Present Record | Pre-vi-ous Record | Present Record | Pre-vi-ous Record |                                                         |
| URNATELLIDAE                        |                |                   |                |                   |                                                         |
| 1. <i>Urnatella gracilis</i> .....  | x              | 0                 | x              | x                 | 0                                                       |
| PALUDICELLIDAE                      |                |                   |                |                   |                                                         |
| 2. <i>Paludicella articulata</i> .. | x              | 0                 | x              | x                 | Cosmopolitan                                            |
| PLUMATELLIDAE                       |                |                   |                |                   |                                                         |
| FREDERICELLINAE                     |                |                   |                |                   |                                                         |
| 3. <i>Fredericella sultana</i> ...  | x              | x                 | x              | x                 | Cosmopolitan                                            |
| PLUMATELLINAE                       |                |                   |                |                   |                                                         |
| <i>Plumatella repens</i> .....      |                | x                 |                | x                 |                                                         |
| 4. phase <i>alpha</i> .....         | x              | 0                 | x              | 0                 | European                                                |
| 5. phase <i>beta</i> .....          | x              | 0                 | x              | 0                 | European                                                |
| 6. var. <i>emarginata</i> ....      | x              | x                 | x              | x                 | Cosmopolitan                                            |
| 7. var. <i>fruticosa</i> .....      | x              | x                 | x              | x                 | European, Asiatic                                       |
| 8. var. <i>furcifer</i> .....       | x              | 0                 | x              | 0                 | European                                                |
| 9. var. <i>appressa</i> .....       | x              | 0                 | x              | x                 | European                                                |
| 10. var. <i>jugalis</i> .....       | x              | 0                 | x              | 0                 | European                                                |
| 11. var. <i>flabellum</i> .....     | x              | 0                 | x              | 0                 | European                                                |
| 12. <i>Hyalinella punctata</i> ...  | x              | x                 | x              | x                 | Cosmopolitan                                            |
| CRISTATELLIDAE                      |                |                   |                |                   |                                                         |
| CRISTATELLA MUCEDO                  |                |                   |                |                   |                                                         |
| 13. var. <i>idae</i> .....          | x              | 0                 | x              | x                 | Status of varieties an unsettled question among workers |
| 14. var. <i>genuina</i> .....       | 0              | x                 | 0              | x                 |                                                         |
| LOPHOPODIDAE                        |                |                   |                |                   |                                                         |
| 15. <i>Lophopodella carteri</i> ..  |                |                   |                |                   |                                                         |
| var. <i>typica</i> .....            | x              | 0                 | x              | *                 | Asiatic, African (?)                                    |
| 16. <i>Pectinatella magnifica</i> . | x              | x                 | x              | x                 | European                                                |

\*Dr. Ulric Dahlgren, of Princeton University, in a recent issue of *Science* (Vol. 79, No. 2057, p. 510, June 1, 1934) reported the occurrence of "*Lophodella carterii* Hyatt 1881" in North America. This is undoubtedly the same form as that which I have listed as var. *typica* in an article entitled "Studies on Freshwater Bryozoa. 1. The Occurrence of *Lophopodella carteri* (Hyatt) in North America," which was accepted in January, 1934, for publication by the Transactions of the American Microscopical Society and which is scheduled to appear in the October (1934) issue of the Transactions.

# STUDIES IN THE BIOLOGY OF THE LEECH. III

## THE INFLUENCES OF CHANGE IN TEMPERATURE UPON LOCOMOTION

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### FORWARD LOCOMOTION

Locomotion in the leech may be differentiated into the following types: First, movements of reptation, i.e., the elongation and shortening of different somites. This includes normal creeping or crawling movements, and looping. Second, movements of undulation as expressed in swimming.

#### A. MOVEMENTS OF REPTATION

True reptation is accomplished by the contraction of the circular muscles followed by a contraction of the longitudinal muscles. In forward locomotion, by reptation, a wave of contraction of the circular muscles originating in the anterior somites travels posteriorly. This results in the elongation of the animal and a subsequent head movement forward. At this point the anterior sucker usually becomes attached. Following this initial wave of contraction is a corresponding contraction of the longitudinal muscles. This later contraction results in the shortening of the animal. The posterior sucker remains attached throughout the period of extension while the anterior sucker becomes attached during the period of shortening. The suckers are primarily organs of fixation but function in normal crawling and looping.

Looping movements are a modification of the movements of true reptation. These movements consist of the normal elongation of the animal followed by a contraction during which the anterior and posterior suckers are brought close together. This movement resembles that of the measuring worm. In this movement the ventral longitudinal muscles play an important role.

It is axiomatic that the nervous system plays an essential part in the process of locomotion. The sequence of muscle

contraction in the earthworm during locomotion has previously been described, (Bovard, 1918).

The question which we desire to raise next is; what is the relationship in the leech between the neuro-muscular system and the stimuli that will produce a specific mode or rate of response?

#### THE INFLUENCE OF CHANGE IN TEMPERATURE UPON LOCOMOTION

It is well known that the type of behavior expressed by certain animals may be conditioned by temperature. It is further evident that the rate of activity is, within limits, proportional to the temperature. D. F. Miller (1929), clearly demonstrated the relation of temperature to the activity of fly larvae. He found that the rate of locomotion varied directly with the temperature from  $2^{\circ}\text{C}.$  to  $40^{\circ}\text{C}.$ , and inversely with the temperature above that point. Further that the rate of contraction increases directly with the temperature between  $0^{\circ}\text{C}.$  and  $45^{\circ}\text{C}.$

Of the factors influencing locomotion in the leech temperature is the most obvious. With a constant light source and with the leeches partially immersed in water a series of tests were made to determine the influence of temperature changes upon locomotion. Temperatures ranging from  $15^{\circ}\text{C}.$  to  $35^{\circ}\text{C}.$ , were used. Below  $15^{\circ}\text{C}.$ , normal crawling could not be recorded accurately, while above  $35^{\circ}\text{C}.$ , forward locomotion by crawling could not be induced. Beyond this temperature swimming movements replaced normal crawling. The accompanying tables will illustrate the results of these experiments.

The effects of temperature-change, upon the number of extensions is illustrated in Table I, column 2. It should be noted that, the number of extensions increases gradually as the temperature rises from  $15^{\circ}\text{C}.$  to  $25^{\circ}\text{C}.$ , but that within the rise through the next  $3^{\circ}\text{C}.$ , the number of extensions nearly doubles. In the last  $7^{\circ}\text{C}.$ , increase in temperature there is a gradual increase in the number of extensions.

The average length of one extension through a temperature range of from  $15^{\circ}\text{C}.$  to  $35^{\circ}\text{C}.$ , is shown in Table I, column 3. The average length of one extension increases as the temperature increases to  $25^{\circ}\text{C}.$  Further temperature increase results in a rapid decrease in the average length of extension.

The effect of temperature change upon the "rate" of locomotion in the leech is shown in Table I, column 4. The number of centimeters traveled per. second increases as the temperature approaches 28° C., after which the speed of locomotion decreases.

Comparing these experiments on the leech with those on the earthworm I find that the two animals yield nearly the same results.

TABLE I

| Temperature<br>° C. | Number of<br>Extensions<br>Per Second | Average<br>Length of<br>Extension<br>in cm. | Centimeters<br>Per Second |
|---------------------|---------------------------------------|---------------------------------------------|---------------------------|
| 15                  | .26                                   | 1.7                                         | .442                      |
| 18                  | .28                                   | 1.9                                         | .532                      |
| 20                  | .29                                   | 2.2                                         | .638                      |
| 22                  | .31                                   | 2.6                                         | .806                      |
| 25                  | .34                                   | 3.2                                         | 1.088                     |
| 28                  | .51                                   | 2.4                                         | 1.224                     |
| 30                  | .57                                   | 2.0                                         | 1.140                     |
| 33                  | .60                                   | 1.8                                         | 1.080                     |
| 35                  | .63                                   | 1.7                                         | 1.071                     |

#### B. UNDULATORY AND SWIMMING MOVEMENTS

Undulatory movements are common to all leeches. In some these movements are more pronounced than in others. In *Haemopsis marmoratis* (Say) this type of movement is frequently expressed. These movements have been variously described, as respiratory and excretory. So far as I have been able to determine no connection between these so-called "causal movements" and the movements themselves exists.

For convenience of reference I have differentiated between rhythmic movements which result in locomotion, designated, as swimming movements, and movements which occur while the leech is attached posteriorly, designated, as undulatory movements. These two expressions of behavior are fundamentally the same and differ in the rate of contraction depending on the type and intensity of the stimuli.

Either undulatory or swimming movements may be instigated by any one of a variety or combination of stimuli. Those environmental stimuli which proved most successful were: changes in temperature; changes in dissolved oxygen and free carbon-dioxide; mechanical, electrical and chemical changes. Water currents (mechanical) also stimulated rhythmic movements.

TABLE II

| Temperature<br>° C. | Number of<br>Undulations in<br>Swimming<br>per min. | Number of<br>Undulations while<br>Attached<br>per min. |
|---------------------|-----------------------------------------------------|--------------------------------------------------------|
| 10.                 | 0                                                   | 30                                                     |
| 12.5                | 0                                                   | 33                                                     |
| 15.                 | 72                                                  | 35                                                     |
| 17.5                | 76                                                  | 37                                                     |
| 20.                 | 80                                                  | 40                                                     |
| 22.5                | 85                                                  | 45                                                     |
| 25.                 | 91                                                  | 52                                                     |
| 27.5                | 97                                                  | 68                                                     |
| 30                  | 104                                                 | 86                                                     |
| 32.5                | 115                                                 | 0                                                      |
| 35.                 | 130                                                 | 0                                                      |
| 37.5                | 175                                                 | 0                                                      |

Under experimental conditions it is possible to demonstrate that the rate of undulation and swimming movements may be controlled by regulating the temperature (see Table II). A series of experiments in which the dissolved oxygen and free carbon-dioxide content was varied (at a constant temperature of 25° C.), clearly demonstrated that the rate of undulation is not dependent upon the gaseous concentrations in the water but that a change in concentration of dissolved oxygen or free carbon-dioxide may initiate undulations. At low temperatures (below 15° C.) undulatory movements predominate, while at high temperatures (above 30° C.) swimming movements predominate. Temperature at these critical points is a direct factor in determining the type of behavior expressed.

The leeches were placed in a large shallow container which was partly filled with water. This container was immersed in a water bath, the temperature being regulated from the outside. Leeches were first exposed to low temperatures and gradually to higher temperatures. Coordinated movements are replaced by spasmodic contractions as the temperature rises above 35° C.

Table II, gives a comparison of the undulatory and swimming rate at different temperatures. This series of tests employed a range in temperature of from 15° C., to the lethal temperature of 42° C.

### CONCLUSIONS

#### A

1. As the temperature increases between 15° C., and 35° C., the number of forward extensions increases.
2. The average length of extension increases between 15° C., and 25° C., after which further increase in temperature results in a decrease in the length of extension.
3. The rate of crawl increases with a temperature increase to 28° C., beyond which the rate of crawl decreases.
4. Swimming movements replace crawling as the temperature is increased above 30° C.

#### B

1. The rate of undulation and contraction increases with the increase in temperature from 10° C., to 37.5° C.
2. Undulatory movements normally occur at lower temperatures than swimming movements.
3. Undulatory movements are replaced by swimming movements as the temperature is increased above 30° C.
4. Since either undulation or swimming may occur between 15° C., and 30° C., some, at present, unknown factor may determine which form of activity is expressed.

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- Bovard, John F. 1918. The transmission of nervous impulses in relation to locomotion in the earthworm. Univ. Calif. Pub. Zool., Vol. 18, pp. 103-134.
- Gee, Wilson. 1913. The behavior of leeches with special reference to its modifiability. Univ. Calif. Pub. Zool., Vol. 11, 1912-1914, pp. 197-.
- Miller, D. F. 1929. Determining the effects of change in temperature upon the locomotor movements of fly larvae. Jour. Exp. Zool., Vol. 52, No. 2.

## THE OEDOGONIACEAE

### SUPPLEMENTARY PAPER NUMBER ONE

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Further study of collections of *Oedogonium* and *Bulbochaete* from various parts of the world, since the publication of the author's Monograph,<sup>1</sup> seems to warrant the recognition of additional distinct species in the two genera. In subsequent supplements to the Monograph it is proposed to use the following new names and new combinations as definite species.

#### BULBOCHAETE Agardh 1817

1. **B. robusta** (Hirn) Tiffany n. comb.

*B. monile* Wittr. & Lund. var. *robusta* Hirn. Mon.<sup>2</sup> p. 30, Fig. 73.

2. **B. scrobiculata** Tiffany n. comb.

*B. elatior* Pringsh. var. *scrobiculata* Tiffany. Mon. p. 33, fig. 3.

3. **B. woronichini** Tiffany n. nom.

*B. brebissonii* Kuetz. var. *minor* Woronichin. Mon. p. 34.

4. **B. suberecta** (Collins) Tiffany n. comb.

*B. nordstedtii* Wittr. f. *suberecta* Collins. Mon. p. 37, fig. 18.

5. **B. glabra** (Hirn) Tiffany n. comb.

*B. sessilis* Wittr. f. *glabra* Hirn. Mon. p. 39, fig. 20.

6. **B. norvegica** (Wittr.) Tiffany n. comb.

*B. tenuis* (Wittr.) Hirn var. *norvegica* (Wittr.) Hirn. Mon. p. 44, fig. 60.

7. **B. litoralis** (Hirn) Tiffany n. comb.

*B. rhadinospora* Wittr. var. *litoralis* Hirn. Mon. p. 47, fig. 68.

8. **B. reticulata** Nordstedt

*B. insignis* Pringsh. var. *reticulata* (Nordst.) Hirn. Mon. p. 49, fig. 63.

9. **B. regalis** (Wittr.) Tiffany n. comb.

*B. imperialis* Wittr. var. *regalis* Wittr. Mon. p. 49, fig. 65.

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<sup>1</sup>Tiffany, L. H. 1930. *The Oedogoniaceae*, a Monograph including all the known species of *Bulbochaete*, *Oedocladium*, and *Oedogonium*. Published by the Author, Columbus, Ohio.

<sup>2</sup>The abbreviation "Mon." will be used throughout to indicate the above Monograph in which the variety or form is described and figured.

## OEDOGONIUM Link 1820

1. **Oe. vulgare** (Wittr.) Tiffany n. comb.  
*Oe. cryptoporum* Wittr. var. *vulgare* Wittr. Mon. p. 66, fig. 102.
2. **Oe. australe** (G. S. West) Tiffany n. comb.  
*Oe. suecicum* Wittr. var. *australe* (G. S. West) B. H. Smith<sup>3</sup> 1932, p. 193; *Oe. suecicum* f. *australe* G. S. West. Mon. p. 68, fig. 117.
3. **Oe. lemmermannii** Tiffany n. nom.  
*Oe. cardiacum* (Hass.) Wittr. var. *minus* Lemm. Mon. p. 71, fig. 129.
4. **Oe. fennicum** Tiffany n. comb.  
*Oe. intermedium* Wittr. var. *fennicum* Tiffany. Mon. p. 73, fig. 135.
5. **Oe. patulum** Tiffany n. nom.  
*Oe. hirnii* Gutwinski var. *africanum* G. S. West. Mon. p. 73, fig. 138.
6. **Oe. robustum** (West & West) Tiffany n. comb.  
*Oe. fragile* Wittr. var. *robustum* (W. & W.) Tiffany. Mon. p. 75, fig. 146.
7. **Oe. subellipsoideum** Tiffany n. nom.  
*Oe. upsaliense* Wittr. var. *fennicum* Hirn. Mon. p. 78, fig. 158.
8. **Oe. gracilius** (Wittr.) Tiffany n. comb.  
*Oe. plagiosotum* Wittr. var. *gracilius* Wittr. Mon. p. 81, figs. 141 and 142.
9. **Oe. diversum** (Hirn) Tiffany n. comb.  
*Oe. capilliforme* Kuetz.; Wittr. var. *diversum* (Hirn) Tiffany. Mon. p. 82, fig. 178.
10. **Oe. maximum** West  
*Oe. fabulosum* Hirn. var. *maximum* (West) Hirn. Mon. p. 83, figs. 217 and 218.
11. **Oe. paraguayense** Tiffany n. nom.  
*Oe. fabulosum* Hirn var. *punctatum* Lemm. Mon. p. 84.
12. **Oe. angustum** (Hirn) Tiffany n. comb.  
*Oe. grande* Kuetz.; Wittr. var. *angustum* Hirn. Mon. p. 86, figs. 198 and 199.
13. **Oe. majus** (Hansg.) Tiffany n. comb.  
*Oe. grande* Kuetz.; Wittr. var. *majus* Hansg. Mon. p. 86, fig. 197.
14. **Oe. amplum** Magnus & Wille  
*Oe. crassum* (Hass.) Wittr. var. *amplum* (M. & W.) Hirn. Mon. p. 88, figs. 204 and 205.
15. **Oe. longum** Transeau n. comb.  
*Oe. crassum* (Hass.) Wittr. var. *longum* Transeau. Mon. p. 88, fig. 208.
16. **Oe. carolinianum** Tiffany n. nom.  
*Oe. paludosum* (Hass.) Wittr. var. *americanum* Nordst. Mon. p. 90, fig. 233.
17. **Oe. occidentale** (Hirn) Tiffany n. comb.  
*Oe. boscii* (Le Clerc) Wittr. var. *occidentale* Hirn. Mon. p. 92, figs. 227 and 228.
18. **Oe. aureum** (Tilden) Tiffany n. comb.  
*Oe. crenulatocostatum* Wittr. var. *aureum* Tilden. Mon. p. 93, fig. 245.

<sup>3</sup>Smith, B. H. Proc. Indiana Academy of Science, 41: 177-206.

19. **Oe. longiarticulatum** (Hansg.) Tiffany n. comb.  
*Oe. crenulatocostatum* Wittr. var. *longiarticulatum* Hansg. Mon. p. 93, figs. 242 and 243.
20. **Oe. paucostriatum** Tiffany n. nom.  
*Oe. paucocostatum* Trans. var. *gracilis* Tiffany. Mon. p. 98, fig. 278.
21. **Oe. abbreviatum** (Hirn) Tiffany n. comb.  
*Oe. pringsheimii* Cramer; Wittr. var. *abbreviatum* Hirn. Mon. p. 107, fig. 331.
22. **Oe. commune** (Hirn) Tiffany n. comb.  
*Oe. nodulosum* Wittr. var. *commune* Hirn. Mon. p. 108, fig. 376.
23. **Oe. epiphyticum** Transeau & Tiffany n. nom.  
*Oe. pisanum* Wittr. var. *gracilis* T. & T. Mon. p. 110, figs. 365 and 366.
24. **Oe. amplius** (W. R. Taylor) Tiffany n. comb.  
*Oe. pyrulum* Wittr. var. *amplius* Taylor. Mon. p. 111, fig. 350.
25. **Oe. hallasiae** Tiffany n. nom.  
*Oe. oblongum* Wittr. f. *sphaericum* (Hallas) Hirn. Mon. p. 117, figs. 368 and 369.  
*Oe. sphaericum* Hallas, preoccupied by *Oe. sphaericum* (Hass.) Kuetz. (De Toni 1889, p. 90).
26. **Oe. sinuatum** Transeau n. nom.  
*Oe. undulatum* (Breb.) Al. Br.; Wittr. var. *americanum* Transeau. Mon. p. 119, fig. 408.
27. **Oe. canadense** Tiffany n. comb.  
*Oe. hystrix* Wittr. var. *canadense* Tiffany. Mon. p. 121, fig. 418.
28. **Oe. subglobosum** (Wittr.) Tiffany n. comb.  
*Oe. hystrix* Wittr. var. *subglobosum* Wittr. Mon. p. 121, fig. 419.
29. **Oe. acutum** (West & West) Tiffany n. comb.  
*Oe. spirale* Hirn. var. *acutum* West & West. Mon. p. 123, fig. 430.
30. **Oe. latviense** Tiffany n. comb.  
*Oe. spirale* Hirn. var. *latviense* Tiffany. Mon. p. 123, fig. 429.
31. **Oe. zehneri** Tiffany n. comb.  
*Oe. braunii* Kuetz.; Pringsh. var. *zehneri* Tiffany. Mon. p. 125, fig. 459.
32. **Oe. angulosum** Hallas  
*Oe. sexangulare* Cleve var. *angulosum* (Hallas) Hirn. Mon. p. 126, figs. 455 and 456.
33. **Oe. subsexangulare** Tiffany n. nom.  
*Oe. sexangulare* Cleve. var. *majus* Wille. Mon. p. 127, fig. 457.
34. **Oe. westii** Tiffany & Brown n. comb.  
*Oe. borisianum* (LeCl.) Wittr. var. *westii* Tiffany & Brown. Mon. p. 128, fig. 470.
35. **Oe. idioandrosporum** (Nordst. & Wittr.) Tiffany n. comb.  
*Oe. crassiusculum* Wittr. var. *idioandrosporum* Nordst. & Wittr. Mon. p. 130, figs. 475 and 476.
36. **Oe. magnum** (Ackley) Tiffany n. comb.  
*Oe. multisporum* Wood var. *magnum* Ackley. Mon. p. 131, fig. 452.

37. **Oe. incertum** Tiffany n. nom.  
*Oe. cyathigerum* Wittr. f. *americanum* Wolle. Mon. p. 134.
38. **Oe. perfectum** (Hirn) Tiffany n. comb.  
*Oe. cyathigerum* Wittr. f. *perfectum* Hirn. Mon. p. 134, figs. 486 and 487.
39. **Oe. striatum** Tiffany n. nom.  
*Oe. wolleanum* Wittr. f. *insigne* (Nordst.) Hirn. Mon. p. 136, figs. 482 and 483.
40. **Oe. rectangulare** (Rich) Tiffany n. comb.  
*Oe. concatenatum* (Hass.) Wittr. var. *rectangulare* Rich. Mon. p. 137, figs. 496 and 497.
41. **Oe. exoticum** (Hirn) Tiffany n. comb.  
*Oe. cleveanum* Wittr. f. *exoticum* Hirn. Mon. p. 138.
42. **Oe. subplenum** Tiffany n. nom.  
*Oe. areschougii* Wittr. var. *americanum* Tiffany. Mon. p. 140, fig. 501.
43. **Oe. pseudoplenum** Tiffany n. nom.  
*Oe. areschougii* f. *robustum* Hirn. Mon. p. 140, figs. 502 and 503.
44. **Oe. exostriatum** Tiffany n. nom.  
*Oe. oelandicum* Wittr.; Hirn f. *minus* Borge. Mon. p. 142, fig. 540.
45. **Oe. senegalense** (Nordst.) Tiffany n. comb.  
*Oe. longicolle* Nordst. var. *senegalense* Nordst. Mon. p. 144, figs. 518 and 519.
46. **Oe. acuminatum** (Hirn) Tiffany n. comb.  
*Oe. macrandrium* Wittr. f. *acuminatum* Hirn. Mon. p. 151, fig. 550.
47. **Oe. borgei** (Hirn) Tiffany n. comb.  
*Oe. monile* Berk. & Harv. f. *borgei* Hirn. Mon. p. 154, fig. 567.
48. **Oe. eminens** (Hirn) Tiffany n. comb.  
*Oe. monile* Berk. & Harv. var. *eminens* Hirn. Mon. p. 154, figs. 568 and 569.
49. **Oe. exmonile** Tiffany n. nom.  
*Oe. monile* Berk. & Harv. f. *victoriense* West. Mon. p. 154, fig. 566.
50. **Oe. completum** (Hirn) Tiffany n. comb.  
*Oe. obtruncatum* Wittr. var. *completum* Hirn. Mon. p. 155, figs. 579-582.

#### Television in Time.

This book is sheer fantasy, reminiscent of Wells, Doyle and Verne at their best. It is scientific fantasy, however, and presents intriguing possibilities of future development in television. In the story, a televisior is devised which when applied to fossils, rocks or other ancient objects, projects about itself a vivid reconstruction of the events which have taken place during the time the object has been exposed to light. The analysis of past events, in which the reader becomes a witness of the actual happenings, moves dramatically across the centuries as continents and oceans form and change, hordes of prehistoric monsters march across the panorama of the years, and the struggle for existence goes ceaselessly on. The book will provide a fascinating evening's entertainment for anyone with a vestige of imagination. L. H. S.

**Before the Dawn**, by John Taine. vii+247 pp. Baltimore, the Williams and Wilkins Co.

# THE ALGAE OF THE URBANA (OHIO) RAISED BOG<sup>1</sup>

FLOYD B. CHAPMAN

Ohio State University

The algae of the Urbana Raised Bog form such an interesting feature of the area, that special effort has been made by the writer to study this aspect of the flora. This unique bog is located at Urbana, Ohio, just north of the Champaign County Fair Grounds. It has been developed around an artesian spring, and due to hydrostatic pressure below and a mat of roots above, has become "raised" or dome-shaped, the center being some ten feet higher than the margins. It is covered with a shrubby type of vegetation consisting chiefly of shrubby cinquefoil (*Dasiphora fruticosa*).

The vascular flora of the bog has been studied by Dr. Robert B. Gordon (2), of the Botany Department at Ohio State University, and it was upon his suggestion that the present work on the algae was undertaken. The first collection of algae was made in early February, 1932, by Gordon, and since that time, much additional material has been obtained, particularly during the spring and summer months of the same year and in 1933. The list of algae from the raised bog is not large, perhaps on account of peculiar environmental conditions which will be discussed in this paper.

The writer wishes to thank Dr. Helen J. Brown and Dr. L. H. Tiffany for aid in identification of certain algae, especially members of the genus *Vaucheria*.

## ALGAL HABITATS

Probably the most important algal habitat at the raised bog is a wide drainage ditch which encircles the entire area. This ditch, during the spring months is well filled with water and remains so until late July, when it becomes much smaller in size. This ditch is fed throughout the year by several springs which flow from the raised bog, and also by a small stream which issues from drainage tiles to the east. In the spring and early summer months the ditch is choked with water-cress (*Sisymbrium nasturtium-aquaticum*;) *Batrachium circinatum*,

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<sup>1</sup>Papers from the Department of Botany, Ohio State University, No. 346.

*Chara foetida*, *Chara fragilis*, and *Zannichelia palustris*. In the early summer months when the water supply decreases, numerous species of herbaceous plants begin to grow along the ditch until the whole is shaded by their dense and rank growth. Most important of these are species of *Carex*, *Rumex*, and *Persicaria*. The ditch remains in this condition until late autumn, when the plants are killed by frost, and the fall rains come. At that time it becomes filled to capacity with water again.

Other interesting situations for algae are the several springs which issue from the bog. The waters of these are cold, clear, and are impregnated with lime. A constant flow of water issues from these springs throughout the year. The temperature of the water is uniformly cool in summer and winter, the temperature being 55° F. on a very hot day in late July. The volume of the springs is diminished to some extent during the summer months, and at that time they are surrounded by various herbaceous plants comprising the same species which grow along the ditch. The shade produced by this dense growth of vegetation is sufficient to prevent growth of algae except, perhaps, some bluegreens and diatoms.

#### SEASONAL CHANGES IN THE ALGAL FLORA

During February, March, and April, the dominant algae are *Tetraspora lubrica*, *Stigeoclonium stagnatile*, *S. subsecundum*, and *Microspora quadrata*. A number of species of *Spirogyra* and one of *Mougeotia* in the vegetative condition are also very common at this season, and persist until May and June when they begin to fruit. All of these occur in the ditch which encircles the bog proper. In April such forms as *Vaucheria sessilis*, *V. woroniniana*, *V. geminata*, and *V. geminata* var. *longistipata* var. nov. appear in the springs. Reproductive structures of *Vaucheria ornithocephala* were found on February 13, 1932. All of these forms usually form a dark green mat on the wet, black muck surrounding the springs, and frequently are found submerged in the flowing water, attached to soil. *Chara foetida* and *C. fragilis* grow in the alkaline waters of the ditch at all times of the year, and both were found fruiting several times in April and again in September. In May, June, and July the dominant forms are the filamentous green algae, comprising the genera *Spirogyra* and *Mougeotia*. Throughout the spring months, *Spirogyra weberi* is exceedingly

common in the ditch. It appears as large yellow-green masses until June, when it turns brownish and begins to produce zygospores. Simultaneously, *Spirogyra varians* var. *scrobiculata* begins to fruit. No zygospore production has been seen in *Mougeotia* collected at this bog, although sterile material is found in abundance, and geniculation frequently occurs, especially in what is perhaps *M. genuflexa*.

Although ditches are usually favorable habitats for representatives of the Oedogoniales, only one species, *Oedogonium landsboroughi*, was collected. Perhaps it is because of the high alkalinity of the waters which flow from beds of marl. The hydrogen-ion concentration of these waters was determined colorimetrically in the field on February 22, 1933. A pH value of 9 was recorded. This fact probably explains the absence of a great many other genera of algae.

In late May, June, and early July a number of blue-greens were found, consisting of species of *Lyngbya* and *Oscillatoria*. These forms were dominant until the vegetation had developed sufficiently to shut out most of the light from the water. They were then succeeded in August and September by enormous quantities of diatoms, which seem to flourish under the conditions of diffuse light, warmer temperatures, and subsequent decay of vegetation. Great masses of iron bacteria form in the ditch in open, sunny places during the hot summer months, accompanying a rapid decay of *Chara* and other water plants.

ANNOTATED LIST OF ALGAE OCCURRING IN THE  
URBANA RAISED BOG

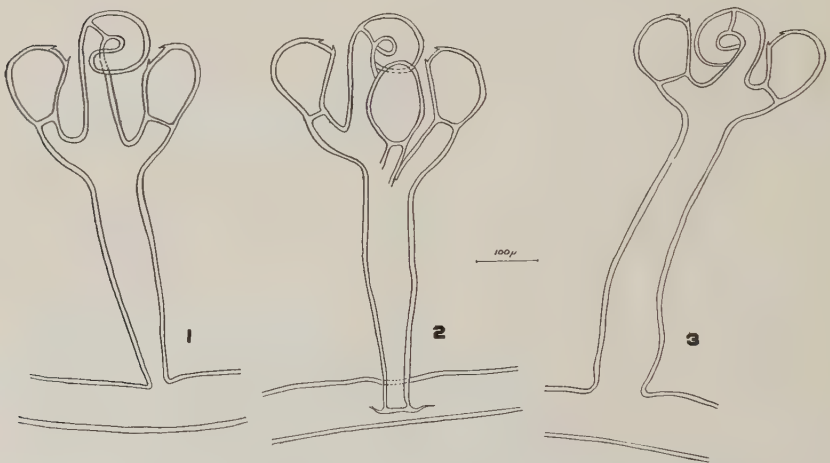
DIATOMACEAE

1. *Nitzschia obtusa* W. Smith. An abundant diatom occurring throughout the year, both in springs and in the ditch.
2. *Achnanthes microcephala* Kütz. Abundant.
3. *Synedra ulna* (Nitzsch.) Ehr. Abundant in autumn and spring.
4. *Cymatopleura solea* (Breb.) W. Smith. Very rare. Spring.
5. *Gomphonema intricatum* Kütz. Abundant. April.
6. *Gomphonema montanum* Schum. Common. September.
7. *Tabellaria fenestrata* (Lyngbh.) Kütz. Common. May.
8. *Fragillaria virescens* Ralfs. Common. September.
9. *Navicula radiosa* Kütz. Particularly abundant in August and September.

CHLOROPHYCEAE

10. *Closterium moniliferum* (Bory) Ehr. Rare. April.
11. *Gonatozygon brebissonii* De Bary var. *minutum* W. & G. S. West. Rare. February.

12. *Stigeoclonium stagnatile* (Hazen.) Collins. Abundant in spring months.
13. *Stigeoclonium subsecundum* Kütz. Common in spring months in the ditch.
14. *Stigeoclonium stagnatile* Kütz. April. Rare.
15. *Rhizoclonium hieroglyphicum* (Ag.) Kütz. April. Common.
16. *Tetraspora lubrica* Ag. Common in the ditch. March-April.
17. *Ulothrix tenerrima* Kütz. Rare in the ditch. April.
18. *Geminella minor* Heering. Rare. May.
19. *Microspora stagnorum* Lagerh. Common in spring months.
20. *Microspora quadrata* Hazen. Abundant in spring months.
21. *Tribonema minus* (Wolle) Hazen. Rare. April.
22. *Stichococcus bacillaris* Näg. Occasional in April.
23. *Spirogyra weberi* Kütz. Abundant in the ditch. Fruits in June.
24. *Spirogyra varians* (Hass.) Kütz. var. *scrobiculata* Stockmayer. Common in the ditch, fruiting in May and June.
25. *Mougeotia genuflexa* (Dill.) Agardh. Common in the spring months. Often geniculating, but never producing zygospores.
26. *Oedogonium landsboroughi* (Hass.) Wittr. Rare, fruiting in May.
27. *Vaucheria sessilis* D. C. Common, fruiting in April.
28. *Vaucheria geminata* D. C. Common, fruiting in May.
29. *Vaucheria geminata* D. C. var. *racemosa* (Vauch.) Walz. Rare. In the springs.



Figs. 1-3. *Vaucheria geminata* D. C. var. *longistipata* var. nov. Figs. 1 and 2 show typical specimens. Fig. 3 represents a minor variation, probably an immature individual, but interesting because of the very long stipe.

30. *Vaucheria geminata* D. C. var. *longistipata* var. nov. (Figs. 1-3).

Latin diagnosis: Filamentis  $80-106\mu$  latis; ramis fructiferis, erectis,  $70-94\mu$  latis,  $320-550\mu$  longis; oogoniis 2-5 (plerumque 2-3) continuis, ovoideis vel oblongo-ovoides, arcuatis, lateraliter sub antheridiis sitis,  $70-89\mu$  latis,  $99-112\mu$  longis; oosporis eadem

forma ac oogoniis, oogonia complentibus, 65-84 $\mu$  latis, 93-105 $\mu$  longis; antheridiis terminalibus, curvatis, 32-38 $\mu$  latis.

Description: Filaments 80-106 $\mu$  in diameter; oogonia and antheridia borne at the end of a long branch, 70-94 $\mu$  in diam., 320-550 $\mu$  long; antheridium terminal, in typical specimens much surpassing the oogonia, hooked or circinate, 32-38 $\mu$  in diam.; oogonia 70-89 $\mu$  wide, 99-112 $\mu$  long, ovoid or oblong-ovoid, arched, 2-5 in number, usually 2-3; beaks of oogonia short; pedicels of oogonia 32-45 $\mu$  long, 32-38 $\mu$  wide, usually arising just below the antheridium, never surpassing it; oospores 65-84 $\mu$  wide, 93-105 $\mu$  long, completely filling the oogonia.

This variety has characters intermediate between *V. woroniniana* and *V. geminata*. It resembles the former in the long pedicel and short oogonial beaks, and the latter both in the number of oogonia and the arched appearance of the oogonia. It differs from both in that the antheridia always surpass the oogonia. In the light of these characters it is questionable whether the plant should be made a variety of *V. geminata* or of *V. woroniniana*. Perhaps there is more evidence for the former since *V. geminata* has long been known to vary in various habitats.

Type locality: Urbana Raised Bog, Champaign County, Ohio. In flowing springs associated with *Vaucheria ornithocephala* and *V. geminata*.

31. *Vaucheria ornithocephala* Ag. Rare. Found fruiting sparsely on February 13, 1932. This species has not been hitherto reported from Ohio.
32. *Vaucheria woroniniana* Heering. Very rare. Found fruiting on February 13, 1932. This species has not been previously reported from Ohio.
33. *Golenkinia paucispina* W. & G. S. West. Common in the ditch in April.

#### MYXOPHYCEAE

34. *Lyngbya major* Menegh. Rare. April.
35. *Lyngbya aerugineo-caerulea* (Kütz.) Gomont. Common in May and June in the ditch.
36. *Oscillatoria tenuis* Agardh. Common in the ditch during the late spring and early summer months.

#### CHARACEAE (CHAROPHYTA)

37. *Chara fragilis* Desvaux. Associated with *C. foetida*. Fruits from April to October.
38. *Chara foetida* A. Br. Abundant in the ditch. Fruiting from April to October.

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### Morbid Inheritance

This book, written by British physicians for physicians and students of human inheritance, attempts to answer three questions frequently asked by those contemplating marriage, or by married couples contemplating parenthood. These questions are "Ought I to get married?" "If I get married, ought I to have children?" "If I get married and have children, what are the chances of their inheriting my disease or a disease which occurs in my family?" It is a sorely needed book, and is very satisfactory as a first attempt. However, it almost completely ignores the important American literature, such as Macklin, Warthin, and Wells on cancer, Kraatz on deaf-mutism, Davenport on goitre, Osborn on baldness, Allan on migraine, etc. Each chapter is by a specialist in the field, and the book contains chapters on nervous disorders, mental disorders and deficiency, diseases and abnormalities of the eye, the ear, the blood, the skin, the heart, the kidneys and the skeleton, cancer, tuberculosis, allergies, diabetes, goitre, and gastro-intestinal diseases. The discussion of each condition is followed by a "eugenic prognosis" for the condition. The treatment is ultra-conservative, which is probably the correct procedure at this stage of our knowledge. The chapter on neoplastic diseases is weak, and not up to the standard of the rest of the volume. The opening chapter by Gates on genetic principles, and the closing one by Hogben on the analysis of pedigrees, are scholarly examples of scientific approach, and add considerably to the value of the book. Every physician and every student of human inheritance should read this work.—L. H. SNYDER.

**Chances of Morbid Inheritance**, by a series of specialists, edited by C. P. Blacker. xi+449 pp. Baltimore, William Wood and Co., 1934.

### Man and the Universe

The demand for popular or survey courses in physical science has become so great that many colleges and universities have felt themselves called upon to insert such courses in their curricula. An immediate consequence of such action is of course that the book market becomes flooded with textbooks allegedly suitable for such courses. This text is just such a one. The subject matter, covering a host of subjects embracing physical science from elementary physics to geology and weather forecasts, is treated in a fashion suitable to about seventh or eighth grade pupils in a public school system, but certainly not as suggested by the authors for college students. The reviewer can well remember as a junior high school pupil having been made to study just some such book in general science, and while the scholastic level of secondary education may indeed since then have dropped to a new law, he can not be convinced that such a book can have any value whatever in a college survey course in physical science. At the institution where the writer is located a survey course in physical science has been attempted. A year's trial has indicated that it merits repetition, but the plane upon which it has been given has been upon a distinctly higher level than that of the book under review. The book comes well bound in cloth and printed on very good paper and in clear type. The book, in the reviewer's opinion, would be suitable for an eighth grade course in general science.—H. H. NIELSEN.

**Man and the Nature of His Physical Universe**, by F. C. Jean, E. C. Harrah and F. L. Herman. x+524 pp. Boston, Ginn and Co., 1934.

## NEW COLEOPTERA (BUPRESTIDAE AND CERAMBYCIDAE)

JOSEF N. KNULL  
Ohio State University

### *Agrilus wenzeli* n. sp.

Resembling *Agrilus egenus* Gory in size, color and general appearance, color uniformly brownish bronze.

Head greenish bronze, convex, without median depression; surface densely punctured becoming slightly rugose on occiput, densely clothed with recumbent white pubescence; antennae when laid along side of pronotum, extending slightly beyond middle, serrate from the fifth joint.

Pronotum wider than long, wider at apex than at base; sides broadly arcuate; marginal carina strongly sinuate; submarginal slightly sinuate; the two carinae joined near base of pronotum; disk convex, with a shallow median depression extending from base two-thirds toward apex; an oblique lateral depression each side; prehumeral carinae well indicated; surface obliquely rugose; lateral depressions with recumbent pubescence. Scutellum transversely carinate.

Elytra constricted near middle, expanded behind middle; sides broadly sinuate, tips obliquely rounded, serrulate; disk slightly flattened, sutural margins elevated in apical third; clothed with short recumbent pubescence which is longer in humeral depressions and along suture, thus giving the appearance of a faint sutural stripe on each elytron.

Abdomen beneath sparsely pubescent; pubescence longer on pro-, meso- and meta-sternum, prosternal lobe broadly rounded; first segment of abdomen flattened, somewhat concave posteriorly, first segment covered with short dense pubescence; anterior and middle tibial mucronate on inside at apex; tarsal claws similar on all feet, cleft, the inner tooth broad, shorter than outer one, not turned inward; male genitalia similar to that of *Agrilus falli* Fisher as figured by Fisher.<sup>1</sup>

Length, 4.75 mm.; width, 1.25 mm.

*Female*.—Differs from the male in having the front of head uniformly reddish cupreous; first two ventral segments of abdomen rounded; the ventral median line of pubescence not as marked; tibiae unarmed.

Type a male labeled Huachuca Mountains, Arizona, July 14. H. A. Wenzel collector, in collection of the writer.

Paratypes labeled Huachuca Mountains, Arizona, July 10, 14, H. A. Wenzel and Palmerlee, Arizona, in the Wenzel Collection at Ohio State University and collection of the writer.

<sup>1</sup>W. S. Fisher, U. S. National Museum, Bull. 145, pp. 1-347, 1928.

I take pleasure in dedicating this species to the late H. W. Wenzel, who presented me with specimens some years ago.

According to Fisher's key, this species would run to *A. chiricahuae* Fisher, but the male genitalia will separate it.

***Mastogenius subcyaneous crenulatus* n. subsp.**

This subspecies resembles *Mastogenius subcyaneous* Lec. in size and shape. It is piceous above and below, with the front less strongly impressed. Pronotum with disk less strongly punctured, crenulate, pubescence arising from punctures longer. Scutellum more elongate. Elytra more densely, coarsely punctured.

Length, 3 mm.; width, 1.2 mm.

Type labeled Clark's Valley. Dauphin Co., Penna., May 24, J. N. Knull, in the collection of the writer.

Paratypes in the U. S. National Museum, the Wenzel Collection at Ohio State University and the collection of the writer as follows: Dunedin, Florida, May 28, W. S. Blatchley; Tybee Island, Georgia, July 8; Southern Pines, North Carolina, May 9, A. H. Manee; Opelousas, Louisiana, Apr. 24; Angelsea, New Jersey; Jeannette, Penna. June 20, H. G. Klages; Manada, Gap, July 11, Mont Alto, July 11, Barbours, May 29, Pennsylvania, J. N. Knull.

Mr. J. P. Darlington, Jr., who kindly compared material with the type series of *Mastogenius* (*Haplostethus*) *subcyaneous* Lec., informs me that there are four specimens in the type series of the Leconte Collection. He states further, that the first specimen in the series which bears a yellow label indicating a western locality, agrees with this subspecies. The other three specimens in the series from the Southern States have blue elytra and black pronotums.

Since Leconte did not designate a type in his series and all four specimens can be considered cotypes, I designate number two specimen in the series to be known as the type of *M. subcyaneous* Lec.

***Aneflomorpha parkeri* n. sp.**

Slender, testaceous, moderately shining; entire dorsal surface clothed with long cinereous recumbent pubescence.

Head coarsely punctured; eyes moderately large, granulate; antennae with one and one-half joints extending beyond apices of elytra when laid back over dorsal surface, second joint about as broad as long, third joint longer than fourth, fifth joint longer than fourth, joints six to eleven of about equal length, eleventh joint slightly longer than tenth, joints beyond first two flattened, third, fourth and fifth joints with small spines on inside at apices, third, fourth, fifth and sixth joints carinate on upper surface; surface of first four joints coarsely punctured, punctures much smaller on outer joints; long flying hairs numerous on inside of first seven joints.

Pronotum about as wide as long, constricted at base and apex, widest in middle; surface coarsely punctured, a lateral depression on each side in middle, surface somewhat obscured by the dense recumbent pubescence which is intermixed with longer erect hairs. Scutellum more densely pubescent than rest of dorsal surface.

Elytra with sides nearly parallel; suture of each elytron produced into a stout apical spine; surface coarsely punctured at base, punctures less evident toward apices, recumbent pubescence intermixed with longer erect hairs.

Ventral surface covered with long recumbent white pubescence, intermixed with longer hairs; pubescence on legs corresponding to that on ventral surface.

Length, 16.5 mm.; width, 3.5 mm.

Described from a specimen labeled Pinal Mountains, Arizona, Aug. 12, F. H. Parker, Type in writer's collection.

This species can be distinguished from other members in the genus by the prolonged elytral apices.

***Aneflus fisheri* n. sp.**

Resembling *Aneflus sonoranus* Csy. in size, color and form.

Testaceous, clothed above and below with recumbent cinereous pubescence, with round denuded areas, from the centers of which arise longer hairs.

Head coarsely punctured; eyes prominent, coarsely granulate; antennae reaching slightly beyond the middle of elytra in the female when laid back over the dorsal surface, and nearly to the tips in the male, second joint as broad as long, third longer than fourth, fifth joint longer than fourth, joints five to eleven of about equal length, eleventh joint longer than tenth, first three joints globular, remaining joints flattened, joints four to eleven carinate, carinae becoming stronger on outer joints, inner apical angles of third, fourth, fifth, sixth and seventh joints spinose.

Pronotum longer than wide, more constricted at apex than at base; sides broadly arcuate; surface convex, coarsely punctured, the punctures concealed by the vestiture. Scutellum densely pubescent.

Elytra with sides nearly parallel; apices truncate, bispinose; surface coarsely punctured basally, punctures finer toward apices, somewhat concealed by the vestiture, three rows of round denuded areas on each elytron, a large puncture in the center of each bare space, from which arises a long suberect hair.

Length, 26 mm.; width, 5 mm.

Type a male labeled Globe, Arizona, July 10, F. H. Parker, in the collection of the writer.

Paratypes in the U. S. National Museum, number 50389, and the collection of the writer as follows:

Tucson, Arizona, July, G. Hofer; Tucson, Arizona, July 13, J. F. Tucker; Sabino Canyon, Arizona July 12, 15, 18, 29, Aug. 6, 10, at light, G. Hofer; Hopkins U. S. 8229, Santa Catalina Mountains, Arizona, Aug. 24, at light, M. Chrisman; Oracle, Arizona, July 23, Hubbard and Schwarz; Allende, Mexico, Oct. A. Busck.

This species comes close to *Aneflus sonoranus* Csy. but can be distinguished from this species by the narrower form, absence of elytral costae and presence of the denuded areas on the elytra.

The writer takes pleasure in dedicating this species to Mr. W. S. Fisher, who kindly loaned material from the National Collection for this paper and compared specimens with types in his charge.

***Rhopalophora bicolorella* n. sp.**

Resembling *Rhopalophora longipes* Say in size; color varying from entirely fuscous to red pronotum, some of the dark forms have slight traces of lighter areas on bases of elytra.

Head and antennae piceous; front with large well separated punctures, finely strigose on occiput; antennae of male considerably longer than elytra, those of female extending slightly beyond tips of elytra, second joint small, as long as wide, third joint longer than fourth, fifth joint longer than fourth, joints six to eleven inclusive gradually decreasing in length.

Pronotum dark brunneus, cylindrical, longer than wide, widest in the middle, constricted at base and apex; sides regularly arcuate; disk with a slight indication of a tubercle on each side at base; surface containing irregularly coarsely scattered punctures, a stripe of dense recumbent white pubescence on each side of disk. Scutellum triangular.

Elytra fuscous; sides nearly parallel, expanded on apical fifth, hind angles obliquely truncate; disk coarsely punctured throughout, clothed with very short inconspicuous pubescence which is mixed with scattered longer hairs.

Abdomen beneath finely punctured, densely clothed with short pubescence intermixed with longer hairs; prosternum with a round granular opaque area with scattered punctures on each side, area rather variable in some specimens and replaced by rugulae.

Length, 11.5 mm.; width, 1.5 mm.

Type a male labeled Palmerlee, Cochise Co., Arizona, July 15, No. 50390, in the U. S. National Museum.

Paratypes in the U. S. National Museum, Wenzel Collection, Ohio State University and the collection of the writer as follows: Fort Grant, Arizona, July 19, Hubbard and Schwarz; Palmerlee, Arizona, July 3, 5, 7, 10 and 14, H. A. Wenzel; Huachuca Mountains, Miller Canyon, Arizona, July 27, H. A. Wenzel; Pinal Mountains, Arizona, July 21, F. H. Parker; Burnett Co., Texas, Hubbard and Schwarz; Carizo Springs, Dimmit Co., Texas, Hubbard and Schwarz; San Antonio, Texas, April 18, Hunter and Pratt.

This species can be separated from *R. longipes* Say by the cylindrical pronotum and coarse punctures. It lacks the transverse rugulae on *R. rugulosus* Lec.

## A GENETIC ANALYSIS OF TASTE DEFICIENCY IN THE AMERICAN NEGRO<sup>1</sup>

B. F. LEE

Ohio State University

The establishment of the unit character nature of taste deficiency for phenyl-thio-carbamide by Snyder (1931-1932) and Salmon and Blakeslee (1931), following Fox's original discovery that taste deficiency actually existed, is one of the more recent developments in the study of human inheritance. The studies of these authors on the inheritance of taste deficiency in man have been confined for the most part to American whites.

Preliminary data collected by the writer on the inheritance of taste deficiency in negroes indicated racial differences in the frequencies of the dominant and recessive genes for taste of phenyl-thio-carbamide. The present attempt at a more extensive and critical analysis of the character in the American negro is an outgrowth of the earlier investigation.

A human character which occurs with a fair frequency in a given population, should be analyzed beyond a mere inspection of the family histories. Although we may evolve a reasonable hypothesis of its hereditary nature from observation, the final proof of the nature of the inheritance must lie in the mathematical analysis of the data on the frequency basis. This mathematical consideration of the frequencies of the allelomorphic genes enables us to predict the proportions of the various kinds of offspring to be expected from the various kinds of matings.

The value and reliability of the figures thus obtained will depend on several criteria, among them the number of individuals studied. This point is taken care of in the probable error. Among other criteria that must be considered are mistakes in technique. Fortunately the character in question is easily determined. The subject either reports a bitter taste or no taste at all is recorded. As a further precaution, all non-tasters were given a second and third sample of the compound.

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<sup>1</sup>Prepared in the genetics laboratory of the Ohio State University, under the direction of Dr. L. H. Snyder.

The crystals were placed on the posterior dorsum of the tongue, in the region of the more sensitive bitter taste buds. The tests include negroes of all ages and both sexes, since recent research has shown that age and sex as well as alkalinity and acidity of the saliva have no effect upon taste deficiency.

A further criterion is the randomness of the sample. The sample in question consists of 3,156 negro individuals, of which 500 were taken from southern schools. The remaining portion is made up of persons taken at random from the negro population of Ohio. The family data and a large number of individuals were collected by the writer and aids in the vicinity of Columbus, Ohio. While a more random sample is possible particularly from the southern states, the present sample serves reasonably well as representing the negro population, since a large number of the northern negro families are recently from the south.

As a final criterion, in checking the validity of the figures, a condition of stable equilibrium must be shown. In the absence of selection a new autosomal factor introduced into a population will produce a condition of stable equilibrium after one generation of random mating. In view of the fact that crossing is still taking place to some extent, as well as some selective mating within the hybrid group, the negro population is not altogether the result of random mating and is consequently not at absolute equilibrium. Therefore any deviations of the observed from the calculated proportions (other criteria being accounted for) may be attributed to continued intermixture as well as some selective mating within the hybrid group.

In order to obviate the need of distinguishing between homozygous and heterozygous dominants in man we apply the frequency method (Snyder, 1932, 1934).

The values below are derived from 3,156 negroes of which 291 (.092) are non-tasters. This is a significantly smaller proportion than that found in the white race (.298 non-tasters).

Assuming taste deficiency to be a simple recessive character and designating the two allelomorphs as T and t respectively,

Let  $p$  = frequency of T

and  $q$  = frequency of t.

then  $p + q = 1$ , and  $p^2 + 2pq =$  tasters (A)

$q^2 =$  non-tasters (B)

$q = \sqrt{B}$ .

For this sample  $q = .305$  and  $p = .695$ .

The total sample of 3,156 negroes includes 124 families. This group consists of 509 individuals of which 60 are non-tasters. For the family group,  $A = .883$  and  $B = .117$ , and

$$q = .343$$

$$p = .657.$$

The probable errors for the ratios of the tasters and non-tasters in the family group and the total sample are as follows:

TABLE I

| SAMPLE            | NON-TASTERS     |
|-------------------|-----------------|
| Total sample..... | .092 $\pm$ .003 |
| Family group..... | .117 $\pm$ .009 |
| Difference.....   | .015 $\pm$ .009 |

The difference in the ratios of tasters and non-tasters in the family group and the total sample is less than three times its probable error. Consequently it is not considered a significant difference, and we may accept the family group as a representative one.

The following chart is a summary of the 124 families studied for the inheritance of taste deficiency for phenyl-thio-carbamide. The sample consists of 509 parents and children.

TABLE II

| MATINGS                                 | CHILDREN                                                                            |  |                                                                |
|-----------------------------------------|-------------------------------------------------------------------------------------|--|----------------------------------------------------------------|
|                                         | Tasters                                                                             |  | Non-Tasters                                                    |
| Taste<br>X<br>Taste                     | no. 184<br>obs. .9109 $\pm$ .013<br>calc. .9350 $\pm$ .006<br>dev. .0241 $\pm$ .014 |  | 18<br>.0891 $\pm$ .013<br>.0650 $\pm$ .006<br>.0241 $\pm$ .014 |
| Taste<br>X<br>Taste deficient           | no. 49<br>obs. .7646 $\pm$ .026<br>calc. .7451 $\pm$ .007<br>dev. .0195 $\pm$ .026  |  | 12<br>.2354 $\pm$ .026<br>.2549 $\pm$ .007<br>.0195 $\pm$ .026 |
| Taste deficient<br>X<br>Taste deficient | no. 0<br>obs. 0.000<br>calc. 0.000<br>dev. 0.000                                    |  | 2<br>1.000<br>1.000<br>0.000                                   |

From the above table it can be seen that the deviations of the observed proportions from the expected proportions are

less than three times their probable errors. As a final check, the observed values for the proportions of tasting and non-tasting offspring of the various matings were compared with the expected proportions on the basis of the p and q ratio from the total sample. The results are shown in Table III.

Here again the observed proportions are near enough the expected proportions to establish the unit character nature of taste deficiency for phenyl-thio-carbamide.

In spite of the fact that intermixture as well as selection within the negro group is taking place, Tables II and III

TABLE III

| MATINGS                                 | CHILDREN                                                     |  |                                              |
|-----------------------------------------|--------------------------------------------------------------|--|----------------------------------------------|
|                                         | Tasters                                                      |  | Non-Tasters                                  |
| Taste<br>×<br>Taste                     | obs. .9109 ± .013<br>calc. .9485 ± .001<br>dev. .0349 ± .013 |  | .0891 ± .013<br>.0542 ± .001<br>.0349 ± .013 |
| Taste<br>×<br>Taste deficient           | obs. .7646 ± .026<br>calc. .7673 ± .003<br>dev. .0027 ± .026 |  | .2354 ± .026<br>.2327 ± .003<br>.0027 ± .026 |
| Taste deficient<br>×<br>Taste deficient | obs. 0.000<br>calc. 0.000<br>dev. 0.000                      |  | 1.000<br>1.000<br>0.000                      |

indicate that an equilibrium in regard to the taste genes has been fairly well established. Since the frequencies in the original negroes and whites undoubtedly differ greatly, a rather high degree of random mating is necessary to approach the equilibrium that the sample indicates. Unfortunately repeated attempts to obtain taste results from West Africa in the region of the forest negroes were of no avail. The only results obtained from Africa were one set from East Africa, and one group from the Egyptian Sudan.

Table IV is a summary of the gene frequency ratios for taste deficiency in the races thus far studied.

In this table the Kenya negroes are not to be looked upon as a true representation of the original negroes brought to America. This group is from East Africa and shows traces of admixture with non-negroid stocks (Hooton, 1931).

The forest negroes, particularly those from the Guinea coast of West Africa, in a large measure made up the parent negro population of America. No results were returned from samples of the compounds sent to this group.

The mixed Indian sample does show the effect of crossing with the whites. The non-tasters increase from .060 in full blooded Indians to .106 in mixed Indians. The American

TABLE IV

| COLLECTORS                       | SAMPLE                       | No.  | TASTERS | NON-TASTERS     | P    | Q    |
|----------------------------------|------------------------------|------|---------|-----------------|------|------|
| Snyder<br>(1932)                 | American<br>whites           | 3643 | .702    | .298 $\pm$ .005 | .455 | .545 |
| Levine and<br>Anderson<br>(1932) | Pure<br>American<br>Indians  | 183  | .940    | .060 $\pm$ .011 | .765 | .244 |
| Levine and<br>Anderson<br>(1932) | Mixed<br>American<br>Indians | 110  | .896    | .106 $\pm$ .019 | .674 | .336 |
| Lee                              | American<br>negroes          | 3156 | .907    | .092 $\pm$ .003 | .697 | .305 |
| Lee                              | Kenya<br>Negroes             | 110  | .919    | .081 $\pm$ .017 | .716 | .284 |
| Lee                              | Egyptian<br>Sudan<br>Natives | 805  | .958    | .042 $\pm$ .001 | .795 | .205 |

negro group presents an increase in the proportion of non-tasters of .011 over the Kenya group, and .050 over the Egyptian Sudan natives, and falls between the American whites on the one hand and the Kenya and Egyptian groups on the other hand. The pure blooded Indians show the lowest proportion of non-tasters. However, the mixed group presents a higher proportion of non-tasters than the American negro sample. This higher percentage might easily be accounted for on the basis of social selection. The action of the social forces of the American people allow for crossing of American Indians and whites more readily than that of negroes and whites. There is, however, considerable doubt that the three smaller samples are truly representative of their respective groups.

This uneven distribution of non-tasters among whites, negroes, and Indians leads to the assumption that a recessive mutation for taste deficiency arose in that group which today presents the highest percent of non-tasters, i. e., the Caucasians. The non-tasters among the negroes and Indians being distinctly low might lead one to believe that they were all originally homozygous tasters, and the recessive factor came about through infiltration with the Caucasians. While such an explanation seems plausible further genetic analysis of human populations is necessary before any conclusions can be drawn.

The analysis of threshold values and the effects of temperature on the various taste reactions are in progress in the laboratory, for the negro groups as well as for the white groups. These results will be published later.

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#### Science and Sanity

Count Korzybski presents in this monumental treatise a point of view, which, if adopted generally, would revolutionize and rationalize our modes of thought. He discusses and illustrates from an enormous variety of situations the desirability and the present (1934) necessity of the employment of a non-Aristotelian, non-elementalistic sematics, in which the concept of non-identity is fundamental. It is only through such a system of psycho-logic reactions that sound scientific thinking may occur and that one may progress from unsanity to sanity.

Count Korzybski shows how many prevalent fallacies and confusions are based upon misconceptions of the nature of language, particularly upon verbalisms dealing with fallacious identification. He deals exhaustively with the nature of verbal, mathematical and scientific symbolisms, and the conditions which give them their representative value. For sane thinking, these symbols should conform as closely as possible to the realities of the nature of the universe and life. To secure such conformity and establish it by training is a very urgent problem of our times. Implications of the outcomes of such training in the solution of scientific, social, and political problems are far-reaching and important.

The author has brought together within the compass of this volume an astounding wealth of material. His discussion of the problem from the physiological, neurological and mathematical points of view has been proclaimed as masterly by many specialists in these fields. The text is difficult; its ideas are new. The reader will find himself struggling with them, but realizing their importance, should adopt them for his own.—JOHN W. PRICE.

**Science and Sanity**, by Alfred Korzybski. A Publication of the International Non-Aristotelian Library Publishing Co. The Science Press, Distributors, Lancaster, Penn. 1933.

## BOOK REVIEWS

### How genes act.

In spite of the wide acceptance of modern genetic theories, the embryologist finds himself frequently doubting the role of the genes in embryonic development. This book, written as an attempt to reconcile the theory of the gene with the deep-seated and fundamental characters of developing organisms, is by one who is himself both a geneticist and an embryologist, and thus peculiarly fitted for such a task. Morgan accepts as complete neither the hypothesis that all the genes are acting all the time in the same way, nor the hypothesis that different batteries of genes come into action as development proceeds. In their place he suggests a third hypothesis, that initial differences in protoplasmic regions affect the activity of the genes, which in turn affect the protoplasm, thus creating a series of reciprocal reactions. This hypothesis is elaborated as the book unfolds, through cleavage, gastrulation, development of isolated blastomeres, and other experimental anomalies, parthenogenesis, regeneration, and the determination of sex. The book does not leave the reader feeling that any of the problems are definitely settled, or even partially solved, but it does raise many pertinent questions, and it does provide genuine stimulation to further thought and research. L. H. S.

**Embryology and Genetics**, by T. H. Morgan. vii+258 pp. New York, Columbia University Press, 1934. \$3.00.

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### Development and its experimental analysis.

From the vast fund of literature on experimental embryology, the authors of this volume have selected the pertinent contributions to early development and differentiation, and by means of careful synthesis and critical evaluation have woven them into a connected whole. Crucial experiments have now been performed on many phases of the developmental process, and a book such as this with authoritative interpretations is indeed welcome. A particularly illuminating chapter is devoted to the much-discussed question of the genetic basis of embryology. The book is well illustrated, and the bibliography is arranged in a unique and useful form, giving subject-matter and page of citation in the volume for each reference. Descriptive embryology is rapidly giving way to physiological embryology, and thanks to volumes such as this, he who runs may read. L. H. S.

**Elements of Experimental Embryology**, by J. S. Huxley and G. R. DeBeer. xiii+514 pp. Cambridge, at the University Press; New York, the Macmillan Co. 1934.

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### Accurate Measurements

The author, a son of Professor A. N. Whitehead, has had an extensive experience in the design, construction and use of precision apparatus, particularly during his years as an expert for the British navy. The result is a book which, in the opinion of the reviewer, should be familiar to every graduate student who hopes to do precision work and which will prove equally valuable to scientists of more extensive experience with instruments.

The sections dealing with the theory of errors presents, rather than the idealized mathematical theory restated, a new kind of treatment of the problem based on design in relation to use. In it the author points out particularly some much neglected facts about the securing of accurate judgments and pointer readings by the observer or manipulator of the instruments. Part II deals with Design, again in a stimulating new way. The book is not addressed to the designing technician, but will be chiefly valuable to all classes of researchers who use instruments of precision.—S. RENSHAW.

**The Design and Use of Instruments and Accurate Mechanisms**, by T. N. Whitehead. xii+283 pp. New York, the Macmillan Co. 1934.

### Biological Principles as Illustrated by the Protozoa

This second edition of a standard work by the dean of American protozoologists gives evidence of considerable reorganization and new material, although the general purpose and plan of the book remain the same. It is today without question the student's best and most reliable source of information on the broader and more fundamental aspects of the life of the Protozoa. The concept of a changing organization influenced by continued metabolism is still the central theme of the book.

To this edition a valuable chapter on ecology and parasitism has been added. The author's decision to omit the *Phytomastigophora* entirely, leaving them to the botanist, will be regretted by many, although it must be admitted, however reluctantly, that this solution of the problem of duplication will probably be generally adopted in time. Typography, paper, and binding of the new book conform to the highest standards.—W. J. KOSTER.

**The Biology of the Protozoa**, by Gary N. Calkins. 2nd edition, 607 pp. Philadelphia, Lea and Febiger. 1933.

### Glacial Geology.

This photo-lithoprint of the author's manuscript is divided into four main parts and is, as the title shows, in a modified outline form. Part I deals with Mountain glaciers and glaciation. Part II handles Continental glaciers and glaciation. Part III considers the Pleistocene glacial succession. Part IV is entitled Miscellaneous and covers the Driftless area, Causes of Pleistocene glaciation, duration of the Quaternary, life of the Pleistocene, and the Economic geology of the Drift. There are 10 plates containing 89 figures; these are well selected and are a very definite addition to the outline. As in any treatment of glacial geology there are points open to argument but this does not deduct from the value of the work. Needless to say it gives the author's **inferences** which he endeavors to keep separate from **observations**, a very excellent idea. It is perhaps unfortunate that this outline had to be reproduced by photo-lithoprint as most of us find typing more difficult to read than printing. This may prove however a good point as it will probably cause the author to revise and enlarge the outline more often than would be the case if it was set up in type. In as far as I know it has a field to itself and should prove very useful to students both in and out of glaciated areas. WILLARD BERRY.

**Outline of Glacial Geology** by F. T. Thwaites. 115 pp., paper bound. Ann Arbor, Edwards Brothers. 1934.

### Within the Atom

A truly delightful book written by H. A. Wilson has appeared under the above title. It is a strictly up-to-date discussion of the progress made since the beginning of the century to solve the riddle of the atom, suitable to be given to the layman or the beginning student. It is delightfully and fascinatingly written, the language of mathematics having been replaced by the language of everyday speech; and while many times reading much like a story or a fairy tale, only very little of the actual meaning of the physics involved is sacrificed. It is an account of the complete collapse of the old concepts of nineteenth century physics and the rise and triumph of the quantum theory, told by a man who himself has played a part in the revolution and who has a clear vision of the direction in which modern physics will head in the future. The book comes durably bound in cloth, printed on good paper in large, clear type, and is sincerely recommended to the reader desiring a glimpse of the physical world as visualized by contemporary physicists. For use in introductory or survey courses so much in demand in colleges and universities at the present time, the reviewer feels it is one of the most suitable that has come to his attention.—H. H. NIELSEN.

**The Mysteries Within the Atom**, by H. A. Wilson. x+146 pp. New York, D. Van Nostrand Co., 1934. \$2.50.